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P. 102, Table 5. Figures in the third column (Beech wood) should read 151, 13, 25, 4, 203, 41.

These revised figures have been supplied Dr van der Drift.

P. 102, third line below Table 5. For "The very low figures. . . yields are reasonable" read "These figures are very much higher than have been obtained elsewhere, but van der Drift stresses that his conversion factor is very approximate."

P. 109. Appendix I

ORIBATEI	
for *Oribatella berlesi*	read *Oribatella berlesei*
for *Ceratozetes gracilis* C.L.K.	read *Ceratozetes gracilis* (Mich.)
for *Spherozetes*	read *Sphaerozetes*
PARASITIFORMES	
for *Oloviseius*	read *Olodiscus*

P. 110.

COLLEMBOLA	
for *Folsomia listeri*	read *Folsomia litsteri*
for *Lepidocyrtus lanuginosus* (Gamelin)	read *Lepidocyrtus lanuginosus* (Gmelin)
for *Sminthurides plumilo*	read *Sminthurides pumilio*
after *Bourletiella bilineata*	add (Bourlet)
THYSANOPTERA	
for *Aelothrips*	read *Aeolothrips*
HEMIPTERA	
for *Anoecia vagrans* (Koch.)	read *Anoecia corni* (Fab.)
for *Pemphigius*	read *Pemphigus*
for *Triphidaphis*	read *Trifidaphis*
COLEOPTERA	
for *Feronia strenus*	read *Feronia strenua*
for *Trogophlaeus*	read *Trogophloeus*
for *Quesius nitipennis*	read *Quedius hyperboreus* Erichson
for *Dryops* (*luridus* Er?)	read *Dryops* (*luridus* Er.?)

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VARIATION IN EARTHWORM NUMBERS WITHIN FIELD POPULATIONS

BY W. J. McL. GUILD
Department of Agricultural and Forest Zoology, University of Edinburgh

(With 3 Figures in the Text)

INTRODUCTION

Recent work has shown that earthworm populations are numerically larger and contain more species than was formerly believed. Field populations of up to three and four hundred thousand per acre and containing up to a dozen species have been described (Evans & Guild 1947, 1948), and some populations exceeding half a million per acre have been recorded. Very high numbers often occur on market-garden soils having a high organic matter content, and unconfirmed reports state that numbers may exceed two million per acre.

When describing populations from agricultural fields, it has been assumed that although these populations differ in size between fields of different agricultural history, they are relatively uniform in distribution over the area in question. Variation in sample numbers has been ascribed to errors of random sampling. More recent work, on field sites with less uniform soil environment than is normally associated with agricultural fields, e.g. Scottish hill pastures (Guild 1951 *a–c*), has shown that where soil conditions are very variable, even within small areas, the distribution of earthworm numbers and species may also be extremely variable. Such variation appears to be in excess of that which might be expected from random sampling in a randomly distributed population, and must be due to the limiting effects of such factors as soil moisture, acidity, herbage cover, etc. In fact, it appears that where the soil environment is variable the populations are divided completely or incompletely into a number of subpopulations whose size and complexity are determined by the limiting factors.

No field area has a uniform soil environment; and as there is always sampling variation, sometimes very considerable, in any earthworm population, it is probable that the term 'normal' or 'average' population has no real significance. Evans & Guild (1947) have shown that seasonal activity within field populations is greatly influenced by soil moisture and soil temperature. Therefore it is probable that these and other environmental factors determine the distribution and subdivision of the total and species populations within any field area at any particular time of year. The object of the present experiment was to determine whether the variation in numbers and species of earthworms could be attributed to random sampling, or whether the variation was due to the existence of smaller units, or subpopulations, within the total population.

EXPERIMENTAL AREA AND METHOD

The experiment was carried out on two areas within the field of Hay Knowes on Boghall Experimental Farm, Midlothian. This field was sown out to grass in spring 1948 and at the time of sampling in autumn 1950 was a well-established, strong-

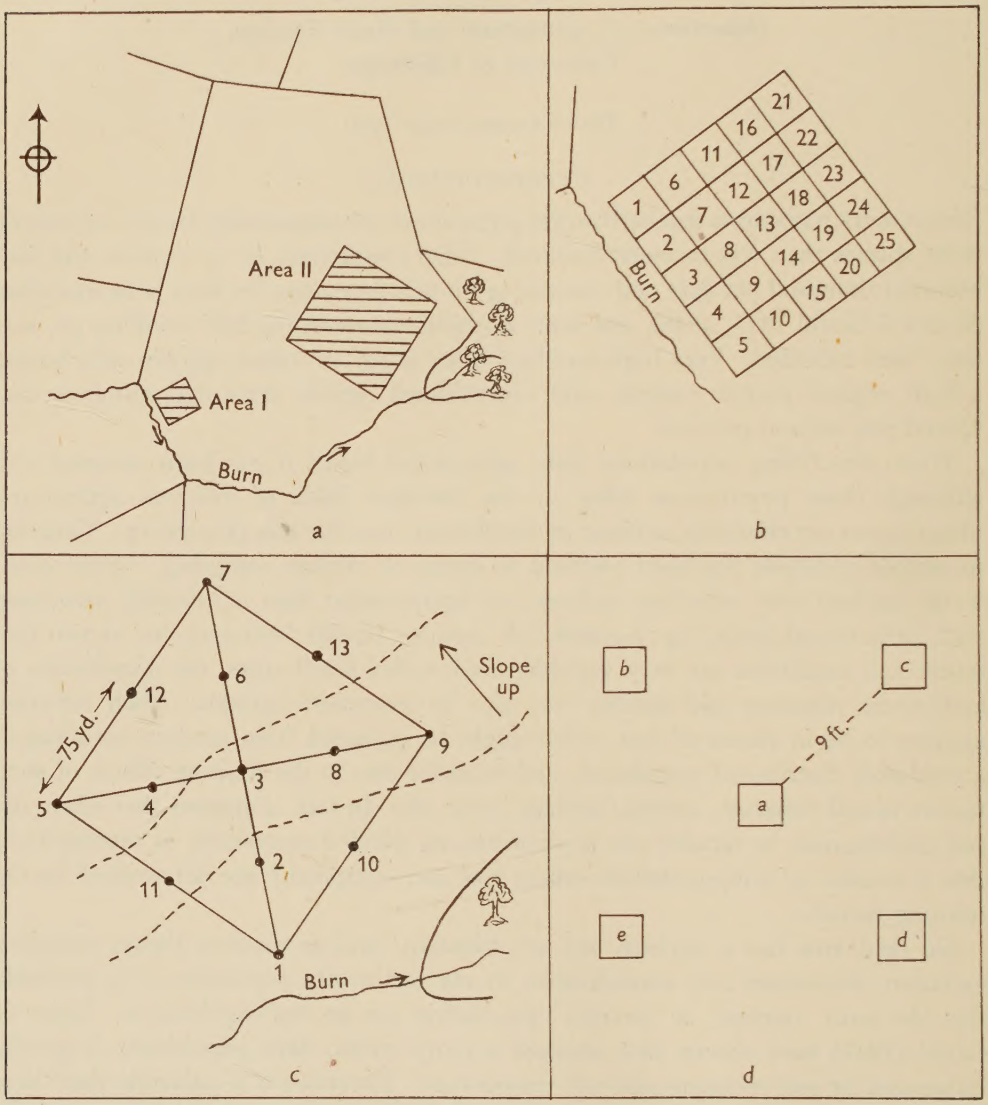

Fig. 1. (*a*) Plan of Hay Knowes (27 acres) showing the positions of experimental Areas I (0·5 acre) and II (4 acres). (*b*) Sampling sites in Area I. Each site is 10 yd. square; four samples, each 3 ft. square, were taken on each site. (*c*) Sampling sites in Area II. (*d*) Positions of samples, each 3 ft. square, taken on each site in Area II.

growing pasture. The elevation is 600 ft. and the soil over the whole field is a medium-light loam with pH 6·7–6·8, giving a field of apparent uniformity as regards soil and general appearance.

Fig. 1 shows the location of the experimental areas. Area I was situated in the south-east corner of the field in the form of a square half an acre in area, on flat ground, with uniform herbage cover. The square was divided into twenty-five squares or sampling sites (5 × 5), each 10 yd. square. Within each of these twenty-five sites four worm samples were taken, each 1 yd. square, giving a total of 100 samples. Area II covered 4 acres, again in the form of a square, and was located on the eastern side of the field. Here the ground was more undulating and a slope down towards the burn passed through the centre of the area. Thirteen sites were sampled, at the corners and on the sides and diagonals of the square, as shown in Fig. 1*c*. Five samples of 1 sq.yd. each were taken at each site, as shown in Fig. 1*d* giving a total of sixty-five samples.

In each area sampling was by the potassium permanganate wet-sampling method (Evans & Guild 1947), the individual samples being kept for separate identification. Area I was sampled during the first 3 days of September, and Area II on the 13th and 14th. During this period the soil conditions, as shown by routine sampling on other fields of the farm, were good for earthworm activity—soil warm, soil moisture approximately 30% and considerable worm activity in the top few inches. Since there was little change in activity trends in other fields during the first 2 weeks in September, the figures obtained on Areas I and II can be compared without much risk of differences between the sample numbers of the two areas being due to seasonal changes in population activity.

Unfortunately, no information on soil temperature or soil moisture was available for Hay Knowes, and discussion must therefore be limited to observed variation within and between the two areas. The variation cannot be related numerically to any particular limiting factor in the environment.

HAY KNOWES POPULATION

An earthworm survey of the field had been carried out a year previously (Guild 1951*a*), and a summary of the results is given in Table 1.

Table 1. *Earthworm population on Hay Knowes, September* 1949

	No./acre (thousands)	Percentage
Allolobophora longa Ude	38·5*	32·1
A. caliginosa Savigny	38·0*	31·7
A. chlorotica Savigny	23·4	19·5
Lumbricus rubellus Hoffmeister	1·8*	1·5
L. terrestris L.	15·7*	13·1
Octoclasium cyaneum Savigny	1·8	1·5
Bimastus eiseni Levinsen	0·8	0·6
Total	120·0	100·0

* Figures from Guild (1951*a*).

Seven species were recorded, of which four: *Lumbricus terrestris* L., and three species of the genus *Allolobophora*, together formed 96·4% of the population. As had been found in many other field populations, *A. longa* Ude and *A. caliginosa* Sav. were the dominant species.

In the present survey a total of ten species was recorded from the two experimental areas. This total included six of the species previously recorded (*Bimastus eiseni* Levinsen being absent), together with *Dendrobaena mammalis* Sav., *Eisenia rosea* Sav., *Lumbricus castaneus* Sav. and *L. festivus* Sav.

Experimental Area I

The numbers of the more important species and the total number of worms collected are shown in Table 2. The population over Area I as a whole was computed from the sample mean $47{\cdot}7 \pm 3{\cdot}0$ ($P = 0{\cdot}05$) and was therefore $230{,}900 \pm 14{,}200$ per acre, unless a one in twenty chance had occurred. With 69% of samples falling within a range of one standard deviation of the mean ($s = 13{\cdot}5$), and as Area I presented to

Table 2. *Earthworm numbers in each of* 100 *samples from Area I*

Site ...	1				2				3				4				5			
Sample ...	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
A. longa	21	48	25	29	36	18	26	19	28	25	23	29	30	30	30	26	16	41	23	16
A. caliginosa	9	8	13	13	7	15	14	24	7	18	15	22	16	18	13	22	3	7	17	10
L. terrestris	2	7	1	3	9	4	8	5	2	6	3	6	7	11	13	10	5	18	11	5
Others	1	5	1	1	2	4	3	2	0	1	1	1	2	2	1	2	0	1	3	2
Total	33	68	40	46	54	41	51	50	37	50	42	58	55	61	57	60	24	67	54	33

Site ...	6				7				8				9				10			
Sample ...	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
A. longa	25	22	27	26	27	16	10	16	31	29	22	13	31	22	39	20	43	48	31	21
A. caliginosa	16	16	25	22	24	13	13	12	13	32	25	21	15	7	27	21	13	18	19	18
L. terrestris	14	8	15	8	8	7	3	5	5	10	7	9	19	11	15	9	12	11	9	4
Others	3	3	1	3	0	3	0	2	2	0	0	0	3	0	2	0	1	2	0	1
Total	58	49	68	59	59	39	26	35	51	71	54	43	68	40	83	50	69	79	59	44

Site ...	11				12				13				14				15			
Sample ...	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
A. longa	41	9	33	13	25	22	26	13	26	13	21	23	26	33	28	13	32	22	20	20
A. caliginosa	9	13	3	11	3	22	6	7	13	11	18	15	23	27	29	20	8	5	12	8
L. terrestris	8	6	12	7	5	6	5	1	14	15	13	5	9	9	6	3	1	2	3	7
Others	0	0	0	1	1	0	1	0	4	2	2	1	5	4	1	4	2	0	0	2
Total	58	28	48	32	34	50	38	21	57	41	54	44	63	73	64	40	43	29	35	37

Site ...	16				17				18				19				20			
Sample ...	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
A. longa	29	27	20	16	46	15	18	18	35	11	29	15	18	20	15	15	21	14	32	16
A. caliginosa	17	26	10	15	22	15	25	19	25	23	14	24	12	13	11	4	4	9	3	7
L. terrestris	9	10	6	5	16	10	10	8	11	10	9	9	4	7	1	2	8	6	5	1
Others	1	3	0	1	0	2	3	1	0	0	0	1	0	1	0	0	0	0	0	0
Total	56	66	36	37	84	42	56	46	71	44	52	49	34	41	27	21	33	29	40	24

Site ...	21				22				23				24				25			
Sample ...	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
A. longa	27	10	19	8	12	10	38	25	25	11	21	20	11	24	12	27	16	25	14	16
A. caliginosa	13	12	20	3	12	10	10	15	22	19	26	29	20	11	12	33	14	21	18	25
L. terrestris	7	7	7	3	5	10	8	10	13	5	14	9	7	14	4	15	4	18	8	8
Others	1	0	0	0	0	0	0	0	0	0	1	2	1	0	1	2	1	2	1	0
Total	48	29	46	14	29	30	56	50	60	35	62	60	39	49	29	77	35	66	41	49

Total $S(x) = 4766$; $\bar{x} = 47{\cdot}7 \pm 1{\cdot}5$; $t_{0{\cdot}05} = 1{\cdot}98$; therefore $\bar{x}_{0{\cdot}05} = 47{\cdot}7 \pm 3{\cdot}0$.

the eye an apparently uniform surface and herbage, it might have been assumed that the population was distributed at random and that the more extreme samples within the total range 84–14 were no more numerous than might be expected in random sampling.

However, Hay Knowes is not a perfectly flat and uniform field, but is undulating in parts. There was therefore bound to be an uneven distribution of drainage and soil moisture, resulting in variation in soil temperature, aeration and actual herbage cover, so that soil conditions must have varied to some extent throughout the field. The standard deviation ($s = 15{\cdot}0$ or $31{\cdot}4\%$ of $\bar{x}$), was relatively high and so variation greater than that attributable to random sampling was suspected within the Area I population.

An analysis of variance for the Area I samples was carried out (Table 3). It was hoped that this type of analysis would show by the significance or non-significance of the values of F whether or not the samples were drawn from a single population with sample variation due to random distribution (non-significant F), or whether there

Table 3. *Analysis of variance in the total population of Area I*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	99	17,993	—	—
Sites	24	12,191	508	—
Samples	75	5,802	77	6·6

When $n_1 = 24$ and $n_2 = 75$: for $P = 0{\cdot}05$, $F = 1{\cdot}95$;
for $P = 0{\cdot}01$, $F = 2{\cdot}56$.

was subdivision into a number of subpopulations, (significant value of F). The exact extent of subdivision cannot be determined, but some indication may be obtained by fitting fiducial limits to the sample means. The analysis of the Area I sample figures (twenty-five sites each of four samples) shows that it is improbable that the total variation within the area was due to errors of random sampling. The variance ratio was highly significant ($F = 6{\cdot}6$) showing that factors other than sampling must have contributed to the total variation, i.e. soil environment factors such as moisture, temperature, etc., acting together, and that the worms were not randomly distributed. An analysis such as this shows that the total population is heterogeneous, some sites belonging to different subpopulations, while others merge or overlap, but it does not show how the total population is divided or into how many subpopulations. If common variance (77) is assumed for all samples, however, fiducial limits can be set to the sample means of each of the twenty-five sites (Snedecor 1946) and a diagram drawn which gives some indication of significant differences between sites. Fig. 2*a* shows that the means of a number of sites appear to be significantly different from the means of neighbouring sites at the 5% level, while in other instances the overlap of the fiducial limit range is very small and there is a likelihood that they are different. Nevertheless, it is hardly possible to say where one subpopulation begins and another ends for there is obviously considerable overlapping. The subpopulation which includes sites 15, 19 and 20 may be a distinct unit, forming an island of low population, but in general there is a merging together of subpopulations, e.g. the gradual increase

in numbers in the series of sites 7–10, and the series 21–23, although in both cases the means of the two end sites are significantly different. The overlapping or integration of the populations might be likened to the merging of oil droplets on water.

It is not advisable to try to deduce too much from a diagram of this type without possessing measurements of any of the soil factors, but it can be said that even on this small and apparently uniform piece of land the earthworm population exhibits

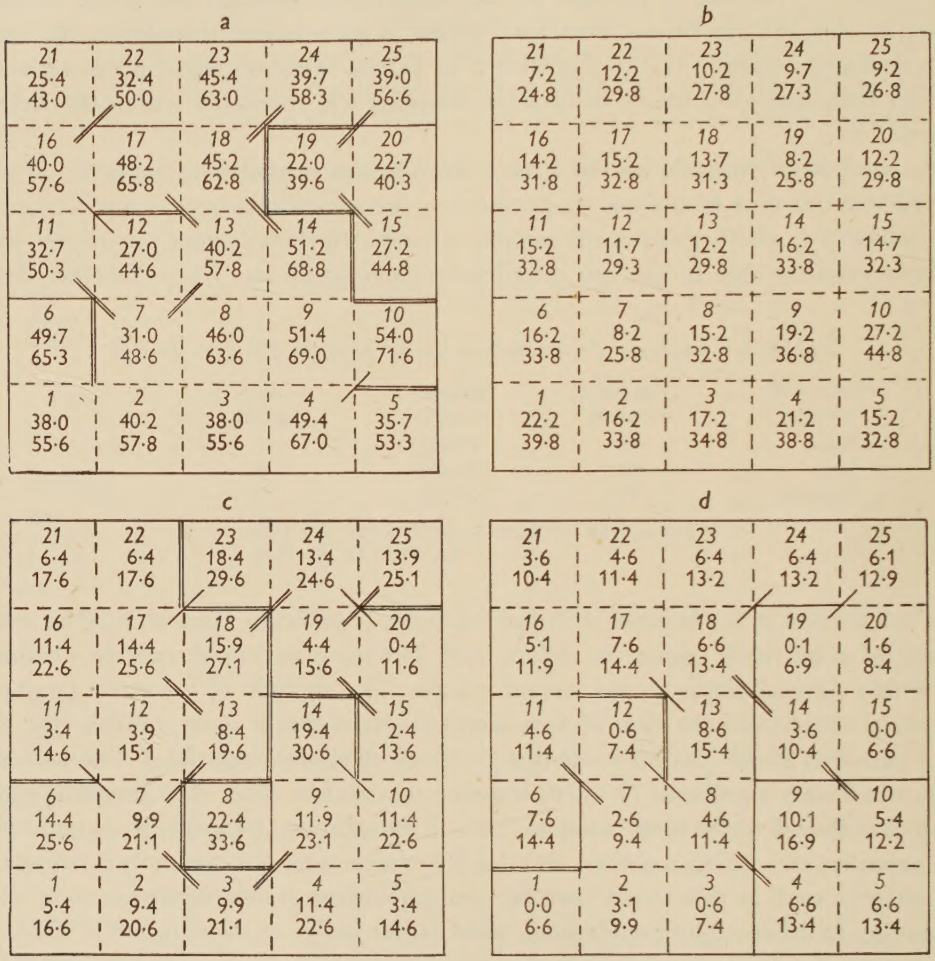

Fig. 2. Fiducial limits to sample-means in Area I assuming common sample variance ($P=0{\cdot}05$). (*a*) Total population: $S_{\bar{x}}t_{0{\cdot}05}=\pm 8{\cdot}8$. (*b*) *Allolobophora longa*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 8{\cdot}8$. (*c*) *A. caliginosa*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 5{\cdot}6$. (*d*) *Lumbricus terrestris*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 3{\cdot}4$. ═══, site-means significantly different; overlap not $>0{\cdot}5$ unit. ——, site-means nearly significantly different; overlap between 0·5 and 2·0 units.

variation and subdivision which is not explained by random sampling, but which is due to variation in soil conditions, or other contributory factors such as the localized grouping of cocoons resulting from aggregation of adults in areas of high organic matter, e.g. dung-pats, old hay-cock bases, etc.

Within the population as a whole the species differ from one another in size, activity and relative abundance, and one or more will be responsible to a greater or lesser degree for the variation exhibited.

Ten species were recorded on Area I but only three of these, *Allolobophora longa*, *A. caliginosa* and *Lumbricus terrestris* were numerous (Table 4). They accounted for 97·7% of the total numbers.

Table 4. *Relative abundance of dominant species* (100 *samples*) *in Area I*

	Number	%
A. longa	2318	48·6
A. caliginosa	1557	32·6
L. terrestris	785	16·5
Others	106	2·3
Total	4766	100·0

The dominant species *Allolobophora longa* and *A. caliginosa* had maintained their positions, the former forming an even higher proportion of the population than in the autumn of 1949. The remaining seven species, which together formed only 2·3% of the total, contained three *Lumbricus* species, *L. castaneus*, *L. festivus* and *L. rubellus*, which have been found to be widely distributed in many places and are usually quite numerous, but in the present instance they totalled only eight individuals (0·2%). None of the other four species was very numerous—*Eisenia rosea* 65 (1·4%), *Octoclasium cyaneum* 31 (0·6%) and *Dendrobaena mammalis* and *Allolobophora chlorotica* one individual each. As these seven species can have played little part in determining the distribution and variation within the total population, the three dominant species must have been responsible.

The numbers of the three dominant species were subjected to an analysis of variance as in the case of total numbers. The dominant species *A. longa*, which comprised about half the population by numbers, had a variance ratio which was not significant at the 1 or 5% levels ($F = 1{\cdot}1$). It would appear, therefore, that this species was probably randomly distributed over Area I and that the variation within the sample range 48–8 was no more than might be expected in sampling from a normal population. Any variations in soil conditions within this area were apparently not sufficient to cause the distribution of *A. longa* to depart substantially from a random distribution. This species was not only dominant numerically with an overall population of $112{,}300 \pm 8700$ per acre ($\bar{x} = 23{\cdot}2 \pm 1{\cdot}8$ at $P = 0{\cdot}05$), but was also dominant on a weight basis, accounting for approximately 75% (3 cwt.) of the estimated total weight of $4{\cdot}0 \pm 0{\cdot}2$ cwt. acre. The distribution of *A. longa* with fiducial limits of the sample means for each site ($P = 0{\cdot}05$) is shown in Fig. 2*b*. Both the species *A. caliginosa* and *Lumbricus terrestris* had highly significant variance ratios at the 1% levels (Table 5), and it appears that the variation in distribution of both these species was greater than would be expected in a normal population. The subdivision of the total population must therefore be mainly due to these species, their distribution being affected by differences in soil conditions not apparent to the eye. This subdivision is shown to some extent in Fig. 2*c* and *d*.

From Fig. 2*b–d* it is seen, first, that in the *Allolobophora longa* population none of the sample means of any of the sites is significantly different from those of adjacent sites or even suggestive of difference. This supports the observations made above that the *A. longa* population is not subdivided. Some support, however, is given to the observations made concerning the subdivision of the *A. caliginosa* and *Lumbricus*

terrestris populations, for there are several places in the diagram where boundaries or probable boundaries could be drawn between different sites, but as in the case of the total population, the subpopulations overlap and merge together.

Table 5. *Analysis of variance of the dominant species in Area I*

	Sum of squares	Variance	*F*
A. longa:			
Total	7825	—	—
Sites	2018	84	—
Samples	5807	77	1·1
A. caliginosa:			
Total	5021	—	—
Sites	2697	112	—
Samples	2324	31	3·6
L. terrestris:			
Total	1683	—	—
Sites	811	33·8	—
Samples	872	11·6	2·9

Degrees of freedom—total = 99; sites = 24; samples = 75.

When $n_1 = 24$ and $n_2 = 75$: for $P = 0{\cdot}05$, $F = 1{\cdot}66$; for $P = 0{\cdot}01$, $F = 2{\cdot}05$.

Experimental Area II

The numbers of the more important species and the total number of worms are shown in Table 6. The total population of this 4-acre area was higher than that of Area I—275,000 ± 22,200 per acre ($\bar{x} = 56{\cdot}8 \pm 5{\cdot}0$ at $P = 0{\cdot}05$), the sample range 119–19, and the standard deviation 20·1 (35·4% of $\bar{x}$) were also higher. An analysis of variance (Table 7) showed that the variance ratio for the total population of Area II was also highly significant at the 1% level ($F = 3{\cdot}9$). The variation in numbers was therefore greater than would be expected from random sampling in a normal population. A significant variance ratio might well have been expected here, for Area II was eight times larger than Area I and the ground was not flat. Sample sites were located on two different levels and on the connecting slope between them (Fig. 1), and as the nature of the ground undoubtedly affected the soil conditions, particularly moisture, this would account for at least part of the variation.

Fig. 3 shows the fiducial limits of the sample means of each of the thirteen sites on Area II, assuming common variance. The subdivision of the population was again indefinite, the boundaries and partial boundaries between sites being incomplete and demonstrating the merging together of the different subpopulations. It is interesting to note that the slope did not affect worm numbers to any extent, both low and high sample numbers being obtained from sites located on it.

The same species were dominant on this area (Table 8) as on Area I, although the percentages of *Allolobophora longa* (38·4%) and *A. caliginosa* (29·2%) and the total percentage of the three species (85·1%), were rather lower. This reduction was mainly due to the species *A. chlorotica*, which, although negligible on Area I, was present in substantial numbers on three sites on Area II and totalled 432 individuals (11·7%). Of the remaining species the three *Lumbricus* species made up 2·0%—*L. rubellus* 63 individuals (1·7%), *L. castaneus* 10 (0·3%) and *L. festivus* one individual.

Table 6. *Earthworm numbers in each of sixty-five samples from Area II*

Site ...	1					2					3					4				
Sample ...	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*
A. longa	10	27	19	12	16	16	14	21	18	5	30	14	20	20	27	27	38	13	18	32
A. caliginosa	10	27	28	29	16	22	9	25	24	21	19	12	13	7	9	37	22	29	14	14
L. terrestris	12	21	7	8	18	18	14	23	12	13	10	10	8	8	14	15	18	12	9	18
Others	1	44	13	3	8	1	0	1	0	0	0	0	1	0	0	2	5	3	0	3
Total	33	119	67	52	58	57	37	70	54	39	59	36	42	35	50	81	83	57	41	67

Site ...	5					6					7					8				
Sample ...	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*
A. longa	19	22	17	40	16	36	30	29	42	34	31	47	36	43	46	32	22	11	24	26
A. caliginosa	11	18	14	20	35	22	14	40	30	27	16	12	14	10	10	4	6	4	3	6
L. terrestris	8	16	11	7	13	8	6	8	9	7	19	9	5	12	7	7	6	6	4	4
Others	1	0	0	0	2	2	4	5	5	2	0	2	1	0	0	43*	18*	35*	36*	43*
Total	39	56	42	67	66	68	54	82	86	70	66	70	56	65	63	86	52	56	67	79

Site ...	9					10					11					12				
Sample ...	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*	*d*	*e*
A. longa	42	22	19	27	16	13	2	15	8	7	8	21	9	18	11	27	20	15	13	15
A. caliginosa	31	16	13	16	10	22	37	22	14	20	20	24	12	17	13	12	6	13	3	2
L. terrestris	12	19	7	4	9	6	0	2	3	4	10	18	5	9	8	5	5	4	3	3
Others	13*	18*	18*	19*	15*	13*	4	11*	7*	2	0	0	0	0	0	0	0	0	0	0
Total	98	75	57	66	50	54	43	50	32	33	38	63	26	44	32	44	31	32	19	20

Site ...	13				
Sample ...	*a*	*b*	*c*	*d*	*e*
A. longa	23	16	19	13	18
A. caliginosa	14	11	15	6	5
L. terrestris	13	20	15	6	10
Others	47	32	23	11	38
Total	97	79	72	36	71

Total $S(x) = 3689$; $\bar{x} = 56{\cdot}8 \pm 2{\cdot}5$. $s = 20{\cdot}1$,
$C = 35\,\%$, $t_{0{\cdot}05} = 2{\cdot}00$, $\bar{x}_{0{\cdot}05} = 56{\cdot}8 \pm 5{\cdot}0$.
Population $= 275{,}000 \pm 22{,}200$ per acre ($P = 0{\cdot}05$).

* Mainly *A. chlorotica*.

Table 7. *Analysis of variance in the total population of Area II*

Source of variation	Degrees of freedom	Sum of squares	Variance	*F*
Total	64	24,799	—	—
Sites	12	11,739	978	—
Samples	52	13,060	251	3·9

When $n_1 = 12$ and $n_2 = 52$: for $P = 0{\cdot}05$, $F = 1{\cdot}94$; for $P = 0{\cdot}01$, $F = 2{\cdot}55$.

Table 8. *Relative abundance of four species (sixty-five samples) on Area II*

	Number	%
A. longa	1417	38·4
A. caliginosa	1075	29·2
L. terrestris	647	17·5
A. chlorotica	432	11·7
Others	118	3·2
Total	3689	100·0

The total was completed by *Eisenia rosea* 34 (0·9%) and *Octoclasium cyaneum* 10 (0·3%).

The variation within the population of Area II must therefore have been due to the distribution of one or more of the four species in Table 8. An analysis of variance

Fig. 3. Fiducial limits to sample-means in Area II assuming common sample variance ($P=0{\cdot}05$). (*a*) Total population; $S_{\bar{x}}t_{0{\cdot}05}=\pm 14{\cdot}0$. (*b*) *Allolobophora longa*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 6{\cdot}4$. (*c*) *A. caliginosa*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 6{\cdot}2$. (*d*) *Lumbricus terrestris*; $S_{\bar{x}}t_{0{\cdot}05}=\pm 4{\cdot}2$. ═══, site-means significantly different; overlap not $>0{\cdot}5$ unit. ——, site-means nearly significantly different; overlap between 0·5 and 2·5 units. – – – –, approximate limits of slope (the same for each diagram).

(Table 9) was carried out for the three dominant species (thirteen sites each of five samples). In each case the variance ratio was highly significant at the 1% level, showing that on Area II the numbers of all three of the dominant species varied more than would be expected from a normal population. These populations must therefore be considered heterogeneous. It should be noted that, whereas on Area I the variance ratio for *A. longa* was not significant, indicating that the soil changes within that small area were not sufficient to cause subdivision of the population, the value of F on Area II was highly significant. The soil environment over this larger area must

therefore have been sufficiently variable to cause subdivision of the *A. longa* population as well as that of the other two dominant species.

Table 9. *Analysis of variance of the dominant species in Area II*

	Sum of squares	Variance	*F*
A. longa:			
Total	7037	—	—
Sites	4374	364·5	—
Samples	2663	51·5	7·8
A. caliginosa:			
Total	5306	—	—
Sites	2784	232	—
Samples	2522	48·5	4·8
L. terrestris:			
Total	2099	—	—
Sites	987	82·3	—
Samples	1112	21·6	3·8

Degrees of freedom—total = 64; sites = 12; samples = 52.
When $n_1 = 12$ and $n_2 = 52$: for $P = 0{\cdot}05$, $F = 1{\cdot}94$; for $P = 0{\cdot}01$, $F = 2{\cdot}55$.

From Fig. 3*c* and *d*, which shows the fiducial limits of the sample means of the three dominant species for each of the thirteen sites ($P = 0{\cdot}05$), it can be seen that there are a number of places where the populations may be subdivided, but there are no clear subdivisions, with the possible exception of the *Allolobophora longa* and *A. caliginosa* populations in the region of sites 6 and 7. In general the *A. longa* population appears to be lower on the flat area at the base of the slope where the soil moisture was highest (sites 1, 2, 10 and 11), while in the same region the *A. caliginosa* numbers were quite high (sites 1, 2 and 10). The *Lumbricus terrestris* population did not appear to be affected by the slope, but there appeared to be a lower population through the centre of the area (sites 12, 6, 8 and 10).

It has now been shown that the populations of both areas I and II are heterogeneous, and it would not be surprising to find that there was a significant difference between the means of the two areas, as recorded above—$47{\cdot}7 \pm 3{\cdot}0$ for Area I and $56{\cdot}8 \pm 5{\cdot}0$ for Area II ($P = 0{\cdot}05$). There is certainly an apparent difference. The standard error of the difference of the means was found to be 2·91, therefore the total partial populations within the same field were significantly different.

DISCUSSION

The Hay Knowes total earthworm population had doubled from the time of the 1949 survey to the time of the present experiment. This was not surprising as earlier work had shown that populations on young rotation pastures build up rapidly after the first year, (Evans & Guild 1947). The three dominant species, which together accounted for over 80% of the numbers, had remained dominant and each had increased in number.

A study of the variation in numbers within the two partial field populations of Areas I and II showed that even on a uniform-looking field like Hay Knowes the increase in numbers of the total population for the field and of the dominant species

within the population was not a simple increase of numbers in a randomly distributed population. The numerical increase of each species, influenced undoubtedly by the changing soil environment throughout the year and throughout the field, resulted in larger total numbers, divided into subpopulations which merged together to form the total population.

The nature of the field, particularly on Area II, indicated that environmental factors such as soil moisture distribution, soil temperature, aeration, herbage cover, etc., would be variable, resulting in a variety of local habitats, large or small, each of different value as feeding or breeding sites, which would account for the uneven distribution and subdivision of the population as a whole. The distribution of the dominant species *Allolobophora longa* was not significantly affected by soil changes in the small area. It is probable that this species, the individuals of which are large, numerous and active, is able to stand greater variation in soil environment, without its distribution departing significantly from normal, than smaller and less active species like *A. caliginosa*, or less numerous ones like *Lumbricus terrestris*. However, the greater variation in the soil environment of the larger area resulted in the distribution of *A. longa* as well as that of the other two species being significantly affected, thereby exhibiting subdivision of the respective species populations, though not necessarily to the same extent or in the same manner, and again resulting in subdivision of the total population. The minor species had a very scattered distribution, some being present in only token numbers. *A. chlorotica*, which was all but absent on Area I, was present in quite substantial numbers on Area II, this increase being almost entirely due to three sizeable colonies. Similarly, with *L. rubellus*, which was in significant on Area I, there were a few sizeable colonies on Area II.

Where enumeration data are obtained from an environment which is affected by many factors, some of which cannot be expressed numerically, e.g. factors comprising a soil environment, it is always difficult and risky to make a strict interpretation of figures obtained from a statistical analysis of the data. Nevertheless, from these experiments and from other quoted works, there is reason to believe that total earthworm populations in the field are subdivided into smaller units, the sizes of which are determined by the limiting factors in the soil. The dominant species are mainly responsible for this subdivision, although their high numbers cause overlapping of subpopulations and obscure the extent of the subdivision. With the less numerous species, overlapping of populations is reduced or eliminated resulting in a series of independent colonies and a few scattered individuals.

SUMMARY

1. Earthworms are not distributed as uniform populations in agricultural fields.

2. Intensive sampling of partial field populations in a field with an overall population exceeding 250,000 per acre shows that the variation in numerical distribution is greater than that which might be expected from random sampling in a uniform population.

3. An analysis of variance for the dominant species and for the total numbers shows that the respective species and total populations are heterogeneous, being divided into subpopulations.

4. The extent of subdivision is difficult to determine, as there is much overlapping, but the size and extent of the subpopulations is affected by: (*a*) the variation in distribution of each of the dominant species within the total population, which may not be the same in all cases, and (*b*) the limiting effects of the factors such as moisture, temperature, aeration, distribution of organic matter, etc., which constitute the soil environment.

5. The species of minor numerical importance are present in isolated colonies, or as scattered individuals, or as both.

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THE BOTTOM FAUNA AND THE FOOD OF FLATFISH OFF THE CUMBERLAND COAST

By N. S. JONES

Marine Biological Station, Port Erin, Isle of Man

(With 1 Figure in the Text)

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INTRODUCTION

The investigations detailed in this paper were undertaken at the suggestion of the Ministry of Agriculture and Fisheries to provide information about the composition of the bottom fauna and its correlation with the food of fishes in an area off the Cumberland coast. Five visits to the area were made in M.V. *William Herdman* during the following periods: 10–11 February 1949, 9–11 March 1949, 17–20 May 1949, 29–30 November 1949, and 22–25 May 1950. Owing to the distance from her base at Port St Mary, Isle of Man, and to the exposed nature of the Cumberland coast, the amount of work accomplished varied with the state of the weather, which was seldom favourable. The area worked was one in which the Ministry of Agriculture and Fisheries research vessel *Platessa* was trawling for plaice during the course of fish-marking experiments. I am most grateful to the scientists aboard her for the provision of the fish guts examined during the investigation, for information concerning positions and duration of trawl hauls, and for their ready co-operation.

METHODS

The bottom fauna was primarily investigated with a 0·1 m.² van Veen bottom-sampler (Thamdrup 1938). The limited time available made a very detailed survey impossible, and during 1949 attention was concentrated largely on the boundaries between different types of bottom. In November 1949 an attempt to obtain ten samples at each of a number of stations was cut short by the onset of strong winds. The weather in May 1950 was good and ten samples were taken at each of eight stations chosen to coincide as nearly as possible with the trawling stations worked by *Platessa*. Positions of stations were fixed by compass-bearings on prominent objects, assisted by the presence of dahn buoys anchored by *Platessa*. Where ten samples were taken at one station, a buoy was anchored and the samples taken within a small radius around the buoy.

Each sample was washed through a sieve with holes 2 mm. in diameter, and the animals preserved in 5% formalin. On returning to Port Erin the animals were sorted, identified, counted and weighed after removing excess moisture. The fauna, after sieving with the aid of a jet of water from a hose, was somewhat broken up, especially in the case of *Amphiura filiformis* which was abundant in many of the samples, but no great difficulty was found in counting this species as the disks remained intact.

In addition, a number of dredge hauls were taken, with a naturalist's dredge on the hard grounds, and on the softer deposits with a runner-dredge fitted with a stramin bag (see Fig. 1 for position of hauls).

A number of guts of plaice and dabs, and a few of soles, were obtained from *Platessa* at various times during 1949. As each haul of her trawl was taken at a known location it was possible to compare the gut contents and the bottom fauna from the station nearest to which the fish were caught. In May 1950 a large number of plaice and dabs were obtained by *Platessa*, and samples of guts from various size-groups of fish were preserved at the same time as the series of bottom samples were taken by *William Herdman*.

The fish guts were examined at Port Erin. In all cases the whole of the gut contents was removed, and the animals present identified and counted. As these were often rather broken, especially in the case of *Cultellus pellucidus*, *Ensis ensis* and *Amphiura filiformis* in the hind parts of the gut, the numbers of each species are somewhat estimated, but it is believed that they are fairly accurate.

THE BOTTOM DEPOSITS

The north-eastern edge of the area corresponds fairly closely with the 5 fm. contour line. The bottom gradually deepens to about 14 fm. at the south-western edge. The deposits fall more or less into four groups: (*a*) In the shallowest part of the area to the north-east is a patch of rough ground consisting mainly of gravel and stones lying on or mixed with muddy sand, with possibly some rock outcrops. There appear to be some isolated portions free from stones. (*b*) The south-eastern part of the area has a bottom of fine sand with little mud. (*c*) Seawards of the rough ground and fine sand, and covering most of the area, the bottom consists of sand mixed with a large proportion of mud. The fine sand grades rapidly into this, and in turn it grades into

(*d*) a pure mud of sticky consistency which extends seawards for an unknown distance. The approximate boundaries are shown in Fig. 1.

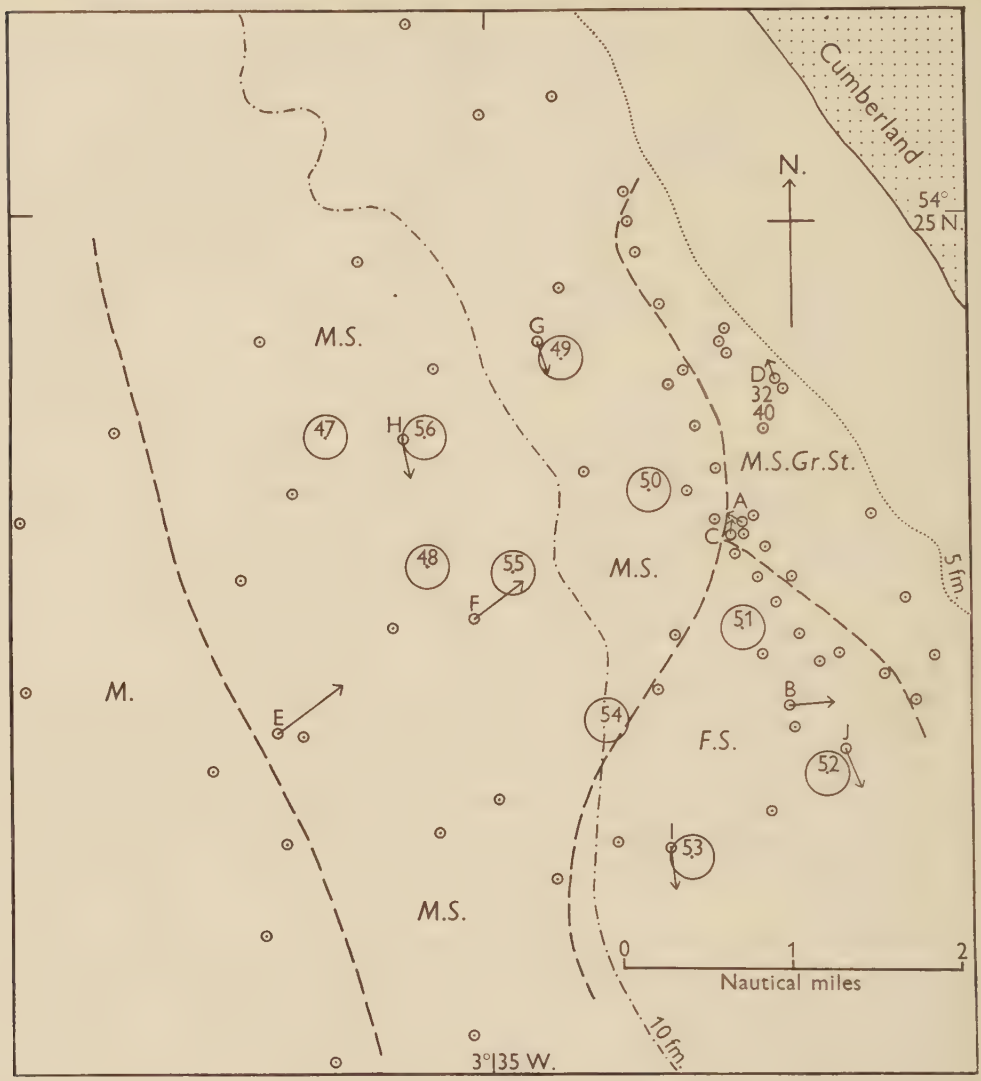

Fig. 1. Map of the area off the Cumberland coast showing positions of hauls and approximate boundaries between grounds. Small circles show positions of single bottom samples, circles with arrows positions of dredge hauls, and large circles areas within which ten samples were taken. Only those stations specifically referred to in the text are numbered. – – –, boundaries between grounds. *M*, mud. *M.S.*, muddy sand. *F.S.*, fine sand. *M.S.Gr.St.*, muddy sand with gravel and stones. ....., 5 fm. line. —·—, 10 fm. line.

HYDROGRAPHY

Temperature and salinity observations were taken on only two occasions using a Nansen-Petterssen water-bottle, with results as follows:

		Temperature (° C.)	Salinity (‰)
11 Mar. 49	Station 32: Surface	5·36	31·897
	Bottom at 6 fm.	5·78	32·347
17 May 49	Station 40: Surface	10·00	32·634
	Bottom at 7 fm.	9·42	32·680

The mean surface temperature in the area over the period 1903–31 was about 5° C. for February, about 10° C. for May, 16° C. for August, and 9° C. for November (Proudman, Lewis & Dennis 1937). The mean surface salinity for the whole year was about 32·5‰ (Proudman 1946).

THE BOTTOM FAUNA

Corresponding to each type of deposit there is a different faunal assemblage. The distribution is shown in Tables 1 and 2. Certain species are common to two or more grounds, but on the whole it is possible to distinguish a separate community for each, particularly if the infauna is considered alone. The epifauna is more widespread.

(*a*) *The fauna of the rough ground*

Owing to the nature of the bottom it was not possible to undertake any quantitative investigations on this ground. Some infauna similar to that on the muddy sand is present in the finer deposits which underlie or are mixed with gravel and stones, but the distinguishing feature of the ground is the presence of a fairly extensive epifauna, though many of the animals included in the latter category occur in smaller numbers on the other grounds, either because they are active and largely independent of the type of substratum or as isolated individuals or groups on scattered oyster shells, etc.

The following are among the more important species:

Alcyonium digitatum	*Pandalina brevirostris*	*Flustra foliacea*
Metridium senile	*Porcellana longicornis*	*Asterias rubens*
Lepidonotus squamatus	*Eupagurus bernhardus*	*Ophiothrix fragilis*
Pomatoceros triqueter	*Hyas araneus*	*Ophiura albida*
Balanus porcatus	*Chlamys opercularis*	*Echinus esculentus*
Pandalus montagui	*Buccinum undatum*	*Psammechinus miliaris*

(*b*) *The fine sand ground*

Infauna. Numerically most important is the lamellibranch *Nucula turgida*, followed by *Cultellus pellucidus*. Also important are *Nephthys* spp., *Sthenelais limicola*, *Venus striatula*, *Abra alba*, *Tellina fabula*, *Ensis ensis*, which is confined to the fine sand, and *Amphiura filiformis*.

Epifauna. Aphrodite aculeata, *Onuphis conchylega*, *Phascolion strombi* in empty *Turritella* shells, *Crangon* spp., *Eupagurus bernhardus*, *Corystes cassivelaunus*, *Macropodia rostrata*, *Aporrhais pes-pelicani*, *Natica poliana*, *Buccinum undatum*, *Philine aperta*, *Asterias rubens*, *Astropecten irregularis*, *Ophiura texturata*, *Psammechinus miliaris* and *Solea lutea*.

The mean rough weight of animals on this ground was 37·5 g./m.^{2} (thirty-seven samples).

(*c*) *The muddy sand ground*

This ground covers most of the area investigated and has a much richer population both in numbers and weight than any of the others. By far the most numerous species in all samples, and making up an important part of the weight of organic matter, was *Amphiura filiformis*. *Echinocardium cordatum* was present in most samples and several species of Polychaeta and Lamellibranchia were important.

Infauna. Nephthys spp., *Owenia fusiformis*, *Pectinaria* spp., *Streblosoma bairdi*, also a small sabellid worm in a mud tube, *Phascolosoma procerum*, *Diastylis* spp., *Ampelisca* spp., *Nucula turgida*, *Thyasira flexuosa*, *Mysella bidentata*, *Venus striatula*, *Cultellus pellucidus*, *Aloidis gibba*, *Turritella communis* in the more muddy parts, *Cylichna cylindracea*, *Amphiura filiformis* and *Echinocardium cordatum*.

Epifauna. Aphrodite aculeata, *Pomatoceros triqueter* on dead oyster shells, etc., *Phascolion strombi*, *Podoceropsis nitida*, *Schistomysis ornata*, *Eupagurus bernhardus*, *Anapagurus laevis* in the more muddy parts, *Aporrhais pes-pelicani*, *Mangelia* sp., *Philine aperta*, *Asterias rubens*, *Ophiura texturata*, *Solea lutea*.

Table 1. *The distribution of the bottom fauna on various grounds off the Cumberland coast*

(The figures show numbers per m.² in the grab samples.)

Bottom deposit	Fine sand	Muddy sand	Mud
No. of samples	37	93	7
COELENTERATA			
Anemone sp.	1·6	1·0	·
NEMERTINEA			
Nemertine spp.	·	4·3	·
POLYCHAETA			
Aphrodite aculeata L.	0·3	1·9	·
Harmothoë spp.	0·8	2·3	·
Sthenelais limicola Ehlers	6·5	3·0	·
Sigalion mathildae Audouin & Edwards	0·3	·	·
Nephthys spp.	11·9	49·6	64·3
Glycera sp.	0·3	2·8	1·4
Goniada maculata Oersted	1·3	0·3	·
Onuphis conchylega Sars	2·2	·	·
Lumbriconereis sp.	3·0	2·6	·
Magelona papillicornis Müller	2·2	0·1	·
Stylarioides plumosa Müller	0·8	0·6	·
Ammotrypane aulogaster Rathke	0·3	0·3	·
Notomastus latericeus Sars	·	1·0	12·9
Owenia fusiformis Della Chiaje	0·3	7·8	·
Pectinaria spp.	·	21·6	·
Amphicteis gunneri (Sars)	0·3	2·5	·
Streblosoma bairdi (Malmgren)	·	29·8	·
Terebellides stroemi Sars	·	4·0	·
Sabellidae	·	51·6	88·6
Other Polychaeta	2·4	2·3	·
GEPHYREA			
Phascolosoma procerum Möbius	·	9·3	·
Phascolion strombi (Montagu)	4·3	3·8	·
Priapulus caudatus Lamarck	·	0·3	·
CRUSTACEA			
Diastylis spp.	0·3	4·0	·
Eudorella emarginata (Kröyer)	·	0·7	·
Cirolana borealis Lilljeborg	·	0·1	·
Ampelisca spp.	2·2	15·0	1·4
Bathyporeia sp.	0·5	·	·
Harpinia antennaria Meinert	3·2	·	·
Photis longicaudata (Bate & Westwood)	·	1·3	·
Siphonoecetes dellavallei Stebbing	1·6	·	·
Other Amphipoda	1·1	0·7	·
Eupagurus bernhardus (L.)	0·8	0·7	·
Jaxea nocturna Nardo	·	0·1	2·9
Corystes cassivelaunus Pennant	0·8	0·4	·
Gonoplax rhomboides (L.)	·	0·9	1·4
Other Decapoda	·	0·3	1·4

Table 1 (*cont.*)

	Fine sand	Muddy sand	Mud
Bottom deposit			
No. of samples	37	93	7
Mollusca			
Nucula turgida Leckenby & Marshall	161·0	11·2	·
Thyasira flexuosa (Montagu)	·	8·3	·
Mysella bidentata (Montagu)	0·3	14·5	·
Cardium echinatum L.	·	1·2	·
Dosinia lupinus (Montagu)	·	0·3	·
Venus striatula (da Costa)	12·2	9·7	·
Gari fervensis (Gmelin)	0·8	0·7	·
Abra alba (Wood)	7·3	4·3	·
A. prismatica (Montagu)	0·3	2·5	1·4
Cultellus pellucidus (Pennant)	51·0	30·1	·
Ensis ensis (L.)	11·6	0·1	·
Tellina fabula Gmelin	4·6	·	·
Mactra corallina (L.)	0·8	·	·
Spisula subtruncata (da Costa)	·	0·7	·
Aloidis gibba (Olivi)	0·3	2·2	·
Other Lamellibranchia	0·3	0·7	·
Turritella communis Risso	·	0·4	·
Natica poliana Forbes	2·4	0·1	·
N. montagui Forbes	0·6	·	·
Buccinum undatum L.	0·6	0·2	·
Cylichna cylindracea (Pennant)	1·1	14·0	·
Philine aperta Ascanius	4·9	10·2	·
Other Gastropoda	0·3	0·2	·
Echinodermata			
Asterias rubens L.	0·3	0·1	·
Astropecten irregularis (Pennant)	1·2	0·1	·
Ophiura spp.	0·8	1·1	·
Amphiura filiformis (Müller)	8·9	919·0	1·4
Echinocardium cordatum (Pennant)	1·2	15·9	·
Leptosynapta inhaerens (Müller)	0·3	2·0	·
Other Echinodermata	·	0·1	·
Total	322	1277	177
Mean weight (g.)	37·5	225·1	18·6

A number of species, including *Cultellus*, become scarcer as the amount of mud in the deposit increases.

The mean rough weight of animals (excluding occasional specimens of *Cardium echinatum* and *Buccinum undatum*, and with gut contents of *Echinocardium* removed) was 225·1 g./m.^{2} (ninety-three samples).

(*d*) *The mud ground*

The mud is poor both in species and weight of organic matter. Only a few samples were taken but in all there was a considerable contrast between this fauna and that of the neighbouring muddy sand. The following are most important: *Nephthys* sp., *Notomastus latericeus*, Sabellidae sp. indet., *Jaxea nocturna*, *Gonoplax rhomboides* and *Abra prismatica*. In addition, *Nephrops norvegicus* was trawled in some quantity.

The mean rough weight was 18·6 g./m.^{2} (seven samples).

The fauna is on the whole similar to that on similar grounds off the south of the Isle of Man, but the biomass is considerably higher and several species are much more abundant off the Cumberland coast. Some minor differences exist between the two areas. *Abra alba* is moderately abundant on both fine and muddy sand off the

Table 2. *Dredge hauls off the Cumberland coast*

(Figures show numbers of specimens per haul: F. = few, C. = common, A. = abundant; N.D. = naturalist's dredge, R.D. = runner-dredge.)

Type of ground ...	Stones and gravel			Fine sand			Muddy sand			
	10 Feb. 49	11 Mar. 49	11 Mar. 49	11 Mar. 49	24 May 50	24 May 50	17 May 49	17 May 49	24 May 50	24 May 50
Instrument	N.D.	N.D.	N.D.	N.D.	R.D.	R.D.	R.D.	R.D.	R.D.	R.D.
Station	A	C	D	B	J	I	F	E	G	H
Tubularia indivisa L.	F.	·	F.	·	·	·	·	·	·	·
Abietinaria abietina (L.)	·	·	F.	·	·	·	·	·	·	·
Hydrallmania falcata (L.)	·	·	·	·	·	·	C.	·	·	·
Alcyonium digitatum L.	C.	F.	F.	·	·	·	·	·	·	·
Metridium senile (L.)	4	2	5	·	·	·	1	·	·	·
Aphrodite aculeata L.	·	·	·	16	5	2	15	3	26	5
Lepidonotus squamatus (L.)	4	1	2	·	·	·	·	1	·	·
Nereis fucata Savigny	5	1	·	·	·	·	2	·	·	·
Nephthys spp.	·	·	·	·	1	·	7	5	·	·
Onuphis conchylega Sars	·	·	·	·	8	5	·	·	·	·
Pomatoceros triqueter (L.)	C.	C.	·	F.	·	·	C.	C.	·	·
Phascolion strombi (Montagu)	·	·	·	10	6	9	44	99	14	20
Balanus porcatus da Costa	F.	F.	C.	·	·	·	·	·	·	·
Diastylis spp.	·	·	·	·	·	·	20	8	·	6
Ampelisca spp.	·	·	·	·	·	·	28	18	·	2
Melita obtusata (Montagu)	·	·	·	·	·	·	6	22	·	·
Podoceropsis nitida Stimpson	·	·	·	·	4	·	55	8	·	5
Photis longicaudata (Bate & Westwood)	·	·	·	·	·	·	13	4	·	·
Podalirius typicus Kröyer	·	·	·	·	·	·	9	4	·	·
Schistomysis ornata (Sars)	·	·	·	·	·	·	40	98	·	·
Mysidopsis angusta Sars	·	·	·	·	·	·	6	2	·	·
Pandalus montagui Leach	20	4	·	·	·	·	·	1	·	·
Pandalina brevirostris (Rathke)	4	4	2	·	·	·	·	·	·	·
Crangon vulgaris L.	·	·	·	·	2	3	·	·	·	·
C. allmanni Kinahan	1	8	·	·	11	·	·	1	·	·
Philocheras bispinosus (Hailstone & Westwood)	·	·	·	·	·	·	9	4	·	·
Porcellana longicornis (L.)	5	3	6	·	·	1	1	·	·	8
Eupagurus bernhardus (L.)	21	4	2	14	18	6	148	25	34	9
Anapagurus laevis (Thompson)	·	·	·	·	1	1	·	51	·	·

Portunus spp.	3	1	·	1	·	1	1	·	·	·
Corystes cassivelaunus Pennant	·	·	·	69	3	4	·	·	·	·
Macropodia rostrata (L.)	1	·	1	·	6	3	·	2	·	3
Hyas araneus (L.)	4	·	3	2	·	1	·	·	1	·
Nucula turgida Leckenby & Marshall	·	·	·	18	1	1	·	·	·	·
Chlamys opercularis (L.)	1	1	·	1	·	·	·	1	·	·
Cardium echinatum L.	·	·	·	·	·	·	·	·	·	2
Venus striatula (da Costa)	·	·	·	5	·	·	7	3	1	16
Gari fervensis (Gmelin)	·	·	·	1	1	·	·	·	·	·
Cultellus pellucidus (Pennant)	·	·	·	6	·	·	2	1	·	·
Spisula subtruncata (da Costa)	·	·	·	·	·	·	3	1	·	·
Aloidis gibba (Olivi)	·	·	·	·	·	·	4	1	1	29
Turritella communis Risso	·	·	·	·	·	·	5	1470	·	5
Aporrhais pes-pelicani da Costa	·	·	·	5	6	6	4	3	·	4
Natica poliana Forbes	·	1	·	3	1	2	·	·	·	·
Neptunea antiqua (L.)	·	·	·	2	·	·	4	·	1	·
Buccinum undatum L.	3	·	·	8	2	1	·	·	2	1
Mangelia sp.	·	·	·	·	1	·	1	13	2	2
Philine aperta Ascanius	·	·	·	7	2	·	45	32	1	4
Armina loveni (Bergh)	·	·	·	1	·	·	7	·	·	·
Flustra foliacea (L.)	·	·	A.	·	·	·	·	·	·	·
Asterias rubens L.	9	·	5	5	29	31	30	26	39	13
Astropecten irregularis (Pennant)	·	·	·	27	7	4	4	1	3	1
Ophiothrix fragilis (Abildgaard)	C.	A.	1	·	·	·	6	·	·	9
Ophiura texturata Lamarck	·	·	1	93	142	50	142	1	204	290
O. albida Forbes	3	42	2	·	·	·	·	·	·	·
Amphiura filiformis (Müller)	·	·	·	·	·	·	100	5	·	2
Echinus esculentus L.	1	·	2	·	·	·	·	·	·	·
Psammechinus miliaris (Gmelin)	6	6	·	2	3	5	·	·	1	1
Echinocardium cordatum (Pennant)	·	·	·	·	·	·	5	·	2	·
Solea lutea (Risso)	·	·	·	20	2	1	7	8	·	2

Cumberland coast, but was very rare in a recent survey off the Isle of Man (Jones 1951). On the other hand, *A. prismatica* was more common in the latter area. Certain species occurring, although in small numbers, off the Cumberland coast have not been found off the Isle of Man. These include *Priapulus caudatus* and *Jaxea nocturna*. On the contrary, many species obtained off the Isle of Man were not found off the Cumberland coast. The muddy sand fauna off the Cumberland coast shows a striking resemblance to that described for an area in Cardigan Bay by Laurie & Watkin (1922).

No accurate comparison can be made with other geographical locations concerning the value of the area discussed in this paper as a fishing ground. It is perhaps permissible to compare the biomass estimated to occur in different places on the sea bottom, even though the estimations are made by various observers using different collecting instruments, but biomass is not necessarily a reliable guide to the numbers of fish present on any ground. Apart from other considerations, most of the biomass may be made up of unpalatable animals. It can also be seen that the biomass varies greatly on different types of bottom within short distances of one another, and reliable information about the numbers of fish caught is not available for other areas. However, it can probably be stated that the area investigated off the Cumberland coast is potentially a fairly good feeding ground for flatfish.

It has not been possible to investigate any seasonal variations in numbers or weight of the fauna that may exist. However, there are some slight indications that these are not great. Ten samples taken on muddy sand at Station 47 on 30 November 1949 show few important differences from ten samples taken 6 months later on 27 May 1950 at Station 56, about half a mile distant. The respective rough weights were as follows: Station 47—271·8 g./m.^{2} and Station 56—251·1 g. m.^{2}. Numbers of important species: *Nephthys* spp., Station 47—57 m.^{2}, Station 56—45 m.^{2}; *Pectinaria* spp., Station 47—10, Station 56—23; *Ampelisca* spp., Station 47—12, Station 56—5; *Mysella bidentata*, Station 47—24, Station 56—114; *Philine aperta*, Station 47—13, Station 56—9; *Amphiura filiformis*, Station 47—1212, Station 56—1188; *Echinocardium cordatum*, Station 47—8, Station 56—16. The only change which is unlikely to fall within the sampling range is that in *Mysella*, of which a new brood had apparently appeared at the time of the second series of samples, the great majority of the specimens being of the **O**-group. No doubt there are annual fluctuations in the numbers of certain species.

THE FOOD OF FLATFISH

After examining the contents of a number of guts it became evident that there was a considerable difference between the feeding of dabs and plaice caught on fine sand and those on muddy sand. The fish from the two grounds are therefore treated separately. Table 3 shows the percentage by number of each food species in gut contents of each species of fish examined from the two grounds. Results for a few soles are included but these have not been allotted to grounds. The number of empty guts is small for all three species. The fish were nearly all more than 15 cm. in length.

(*a*) *Plaice* (Pleuronectes platessa)

The most important food organisms on both fine and muddy sand are various lamellibranchs, particularly *Cultellus pellucidus*, with *Ensis ensis* eaten to a lesser

Table 3. *The percentage contents of fish guts on various grounds off the Cumberland coast*

(The figures opposite each species show its percentage by number of the total contents of the guts of each kind of flatfish on the grounds indicated.)

Fish	Plaice		Dab		Sole
No. of guts ...	366	393	156	250	31
Ground	Fine sand	Muddy sand	Fine sand	Muddy sand	
Nemertine sp.	·	0·06	0·08	·	·
Aphrodite aculeata	·	0·06	2·10	4·50	3·10
Harmothoë sp.	·	0·04	0·08	0·05	0·20
Sthenelais limicola	0·03	0·02	·	·	·
Eunereis longissima	·	0·02	·	·	·
Nephthys spp.	0·34	1·01	0·40	0·40	0·50
Glycera sp.	·	0·27	·	·	·
Goniada maculata	0·06	0·08	·	·	·
Lumbriconereis sp.	·	0·02	·	·	·
Owenia fusiformis	0·02	0·10	·	0·10	·
Ammotrypane aulogaster	·	0·06	·	·	·
Pectinaria spp.	0·20	3·00	0·08	1·00	0·50
Scalibregma inflatum	·	1·68	·	·	·
Amphicteis gunneri	·	0·08	·	·	·
Terebellides stroemi	0·50	8·64	0·40	0·10	·
Other Polychaeta	0·02	0·12	0·20	0·30	·
Phascolosoma procerum	·	·	0·20	·	·
Priapulus caudatus	·	0·17	·	0·05	·
Diastylis spp.	·	0·10	·	0·10	·
Ampelisca spp.	2·04	8·45	1·10	2·50	21·10
Photis longicaudata	·	0·06	0·20	0·20	·
Pordoceropsis nitida	·	·	·	0·05	·
Cirolana borealis	0·02	·	0·08	·	0·20
Eupagurus bernhardus	·	0·02	4·30	3·50	·
Anapagurus laevis	·	·	·	0·10	·
Gonoplax rhomboides	·	·	0·08	0·50	·
Corystes cassivelaunus	0·02	0·04	0·60	0·40	·
Portunus sp.	·	·	·	0·05	·
Hyas coarctatus	·	·	0·08	·	·
Macropodia rostrata	·	·	·	0·60	·
Pandalina brevirostris	0·02	0·15	·	·	·
Crangon sp.	·	0·02	·	·	0·20
Other Decapoda	·	·	0·20	0·20	·
Nucula turgida	1·89	0·38	0·20	0·05	·
Mysella bidentata	·	0·06	·	0·40	0·20
Chlamys opercularis	·	·	0·80	0·30	·
Cardium echinatum (foot)	0·03	0·08	0·30	0·70	·
Venus striatula	0·06	0·04	0·08	·	·
Gari fervensis	0·03	0·31	0·08	0·05	·
Abra alba	1·07	19·47	3·60	0·40	0·50
A. prismatica	·	0·02	·	·	·
Thyasira flexuosa	·	·	·	0·05	·
Spisula subtruncata	0·08	0·12	·	0·10	·
Cultellus pellucidus	81·77	42·14	70·00	25·70	20·00
Ensis ensis	11·22	1·66	5·70	0·40	·
Aloidis gibba	·	0·02	·	·	0·20
Turritella communis	·	·	·	0·05	·
Mangelia sp.	0·02	·	·	·	·
Buccinum undatum (syphon)	·	0·02	0·20	·	·
Cylichna cylindracea	·	0·08	·	0·05	0·20
Philine aperta	·	0·17	4·50	11·60	12·10
Other Mollusca	·	·	0·08	0·10	·
Ophiothrix fragilis	·	·	·	0·20	·
Ophiura spp.	·	·	0·60	0·30	·
Amphiura filiformis	0·53	11·11	3·90	44·90	40·50
Echinocardium cordatum	·	·	·	0·10	·
Leptosynapta inhaerens	·	0·04	·	·	·
Ascidian sp.	·	·	0·08	·	·
Gobius sp.	·	·	·	·	0·20
Fish eggs	·	·	0·08	0·10	·
Total no. of organisms	5136	5227	1295	1932	422
No. of guts empty	3	13	3	7	2
Mean no. of animals per gut	14	13	8	8	14

Table 4. *The distribution of the bottom fauna off the Cumberland coast, 23 May 1950*

(The figures opposite each species show its percentage by number of all animals present in ten samples from each station.)

Station	52	53	51	54	50	55	49	56
Aphrodite aculeata	·	·	0·4	0·3	0·3	·	0·2	0·1
Nephthys spp.	3·8	3·9	3·9	4·5	4·4	4·6	3·2	2·8
Goniada maculata	0·6	1·3	·	0·1	·	·	·	·
Owenia fusiformis	·	0·4	·	0·9	0·8	1·4	0·8	0·4
Pectinaria spp.	·	·	·	2·7	2·8	1·4	2·3	1·7
Terebellides stroemi	·	·	·	0·1	·	·	0·1	0·1
Diastylis spp.	·	·	0·4	0·1	·	0·4	0·4	0·3
Ampelisca spp.	·	0·9	0·7	1·5	1·5	1·6	0·6	0·4
Cirolana borealis	·	·	·	·	0·1	·	·	·
Corystes cassivelaunus	0·3	·	·	0·3	·	·	·	·
Nucula turgida	48·7	41·5	41·6	4·3	1·2	0·7	·	·
Mysella bidentata	·	·	0·4	0·3	0·9	1·3	0·5	0·5
Gari fervensis	0·3	·	·	0·5	0·2	·	·	·
Abra alba	0·3	0·4	0·7	0·3	0·7	1·1	·	0·1
A. prismatica	·	·	·	0·5	0·2	0·2	0·5	0·1
Cultellus pellucidus	15·9	14·5	24·4	6·9	2·5	11·1	·	·
Ensis ensis	3·8	4·3	6·1	0·1	·	·	·	·
Cylichna cylindracea	·	0·4	1·1	3·6	3·2	2·1	1·4	0·1
Philine aperta	3·5	1·7	0·7	0·9	0·8	0·6	1·7	0·6
Amphiura filiformis	2·9	6·4	2·1	64·5	69·7	63·3	81·4	88·3
Leptosynapta inhaerens	·	·	·	0·8	0·2	0·1	·	·
Anemone sp.	0·6	0·9	·	0·4	0·2	0·1	·	·
Nemertine spp.	·	·	·	0·6	0·4	0·4	0·7	0·3
Harmothoë sp.	0·3	0·9	·	0·9	0·2	0·3	·	0·1
Sthenelais limicola	1·8	2·6	3·9	0·9	0·3	1·2	0·1	·
Sigalion mathildae	·	0·4	·	·	·	·	·	·
Glycera sp.	·	·	·	·	0·2	0·3	0·1	0·1
Onuphis conchylega	0·9	0·9	1·1	·	·	·	·	·
Lumbriconereis sp.	1·2	0·4	·	·	·	·	0·1	·
Magelona papillicornis	1·5	0·9	0·4	0·1	·	·	·	·
Streblosoma bairdi	·	·	·	2·3	2·6	2·1	1·6	1·6
Other Polychaeta	1·2	1·7	0·7	1·2	0·2	0·3	0·4	0·1

Phascolosoma procerum	·	·	·	0·5	0·4	0·5	1·3	0·7
Phascolion strombi	0·9	1·7	2·5	0·4	0·4	0·5	0·1	0·2
Priapulus caudatus	·	·	·	·	0·1	·	·	·
Eudorella emarginata	·	·	·	·	0·1	·	0·5	·
Bathyporeia sp.	0·3	0·4	·	·	·	·	·	·
Harpinia antennaria	1·2	3·4	·	·	·	·	·	·
Siphonoecetes dellavallei	·	2·1	0·4	·	·	·	·	·
Other Amphipoda	·	1·3	·	0·1	0·1	0·3	·	·
Upogebia deltaura	·	·	·	·	·	0·1	·	·
Eupagurus bernhardus	·	0·4	0·4	0·6	0·1	·	·	·
Gonoplax rhomboides	·	·	·	0·1	·	·	·	·
Thyasira flexuosa	·	·	·	2·1	2·7	1·0	0·1	·
Cardium echinatum	·	·	·	·	0·2	0·1	0·1	·
Mactra corallina	0·6	·	·	·	·	·	·	·
Venus striatula	3·2	2·1	4·7	0·8	0·4	1·1	0·5	0·1
Aloidis gibba	·	·	·	0·3	0·1	·	·	0·1
Tellina fabula	3·2	1·7	1·1	·	·	·	·	·
Other Lamellibranchia	0·3	·	·	0·3	0·2	0·1	0·1	·
Turritella communis	·	·	·	·	·	0·1	·	·
Natica poliana	0·9	1·7	·	·	·	·	·	·
N. montagui	0·3	·	0·4	·	·	·	·	·
Buccinum undatum	·	0·4	·	·	·	·	·	·
Asterias rubens	0·3	·	·	·	·	·	·	·
Astropecten irregularis	·	·	0·7	0·1	·	·	·	·
Ophiura spp.	·	·	0·7	0·1	·	·	0·2	·
Echinocardium cordatum	0·3	0·4	0·4	1·1	1·9	1·6	1·5	1·2
Total number per m.²	314	234	279	749	1061	1126	1358	1346
Total weight (g.) per m.²	48·4	48·1	40·1	180·6	234·1	214·9	275·3	251·1

extent on fine sand and *Abra alba* on muddy sand. *Nucula turgida* is occasionally eaten on fine sand. Of other animals *Ampelisca* spp. are eaten on both grounds, though because of their small size they are not a very important item. *Amphiura filiformis* is only very occasionally eaten on fine sand but makes up a more appreciable part of the diet on muddy sand. Of the remainder only *Nephthys* spp., *Pectinaria* spp., *Terebellides stroemi* and *Scalibregma inflatum* are of slight importance on muddy sand.

Terebellides appears in Table 3 among the gut contents on fine sand. It does not occur in this deposit in the area and its inclusion in the table is no doubt due to the fact that the fish which had eaten them were caught in one or more of the hauls which traversed both fine and muddy sand grounds. Alternatively, the fish may have moved on to the fine sand after feeding on the neighbouring muddy sand. Similarly, the presence of *Ensis*, which is confined to fine sand, in the gut contents of fish allotted to muddy sand is probably due to one or both of the same causes.

(*b*) *Dabs* (Limanda limanda)

On fine sand, as with plaice, the most important food species is *Cultellus*, with *Ensis* second in importance. *Abra alba* is eaten in smaller numbers. In contrast to plaice, *Amphiura filiformis* is the most abundant animal in the gut contents on muddy sand, *Cultellus* being of secondary importance, while *Aphrodite aculeata*, *Eupagurus bernhardus* and *Philine aperta* are eaten to an appreciable extent on both grounds. *Ampelisca* spp., appear to be less frequently eaten than by plaice, and with the exception of *Aphrodite*, polychaetes are very seldom taken.

It is evident that dabs are competitors with plaice for food, particularly on the fine sand ground. On the muddy sand, however, competition is less keen and the dabs are better able to utilize the available food supply.

The smaller average number of food organisms per gut in dabs compared with plaice is doubtless due to the smaller mean size of the former in the samples.

(*c*) *Soles* (Solea vulgaris)

The few soles examined were probably mostly taken on muddy sand. The gut contents are very similar to those for dabs on this ground, except that *Ampelisca* spp. assume greater importance, while other Crustacea are absent.

DISCUSSION

For purposes of discussion the results obtained during May 1950 are set out in Tables 4 and 5. They show respectively the fauna obtained at each station expressed for each species as a percentage by number of the total animals present, and the gut contents of plaice caught near each station expressed as a similar percentage.

(*a*) *Faunal results*

Table 4 brings out further the differences between the faunas of the fine and muddy sand grounds. Only three of the sampling positions were on fine sand, i.e. Stations 51, 52 and 53, the other five being on muddy sand, with Station 54 slightly overlapping the boundary between the two grounds. The rise in numbers of organisms and the change over in dominance from lamellibranchs to echinoderms on passing from fine to muddy sand is clearly shown.

Table 5. *Percentage contents of plaice guts off the Cumberland coast, May 1950*

(The figures opposite each species show its percentage by number of the total contents of the guts in each sample.)

Station	52			53			51			54			South of 50			North of 50	55		49
Date	23			23			24	24	23	24			23			23	24		23
Time of commencing haul (G.M.T.)	1620			1830			0550	0550	1200	0745			1345			1010	0930		0830
Length of fish (cm.)	>25	20–25	<20	>25	20–25	<20	>25	<20	Mixed	>25	20–25	<20	>25	20–25	<20	Mixed	>25	20–25	Mixed
No. in sample	20	20	20	20	19	20	20	20	20	20	20	15	20	20	20	20	6	20	20
Aphrodite aculeata	·	·	·	·	·	·	·	·	·	·	·	·	0·2	·	·	·	·	·	0·4
Nephthys spp.	·	·	·	0·2	0·5	0·3	0·6	·	·	·	0·5	·	0·4	·	·	0·8	2·0	0·5	6·8
Goniada maculata	·	0·3	·	·	·	·	·	·	·	·	·	·	·	·	·	0·4	·	·	·
Owenia fusiformis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1·4
Pectinaria spp.	·	·	·	·	·	·	·	·	·	·	0·5	·	1·0	·	·	6·5	·	·	9·6
Terebellides stroemi	0·2	·	·	·	·	·	0·6	·	·	·	·	·	0·2	·	·	1·1	2·0	·	2·5
Other Polychaeta	·	·	0·9	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·5	0·4
Diastylis spp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·4	·	·	0·4
Cirolana borealis	·	·	·	0·2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ampelisca spp.	0·4	·	·	1·1	·	0·7	0·6	1·0	0·3	0·9	3·3	·	2·1	0·7	0·5	5·0	9·8	2·3	4·6
Corystes cassivelaunus	0·2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·4	·	·	0·4
Nucula turgida	7·2	0·3	·	0·6	0·2	0·7	·	·	0·3	0·9	·	·	1·4	·	0·5	·	·	·	·
Mysella bidentata	·	·	·	·	·	·	·	·	·	·	·	·	0·2	·	·	·	·	·	0·7
Gari fervensis	·	·	·	·	·	·	·	·	·	·	·	·	0·2	·	·	·	·	·	0·7
Abra alba	0·6	·	·	·	·	·	·	·	·	·	·	·	0·8	·	·	·	2·0	0·5	3·2
A. prismatica	·	·	·	·	·	·	·	·	·	·	·	·	0·2	·	·	·	·	·	·
Cultellus pellucidus	65·3	83·5	91·0	88·8	91·4	89·1	87·1	88·7	88·0	91·4	84·1	92·6	83·8	97·8	96·1	50·8	72·6	94·9	0·7
Ensis ensis	25·9	16·0	8·1	9·3	7·9	9·2	10·6	10·3	11·4	6·9	7·1	7·4	3·8	1·5	3·4	·	·	·	·
Cylichna cylindracea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·4	·	·	0·4
Philine aperta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·8	·	·	1·1
Amphiura filiformis	0·2	·	·	·	·	·	·	·	·	·	4·4	·	5·5	·	·	33·2	11·8	1·4	68·9
Leptosynapta inhaerens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·7
No. of guts empty	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	3	·	·	·
Mean no. of animals per gut	26	20	12	28	22	15	9	5	18	12	9	5	24	13	10	13	15	11	14

Various criticisms have been made of the validity of the results from faunal sampling by means of the grab. One of these, emphasized by Steven (1930), is that the grab takes a differential sample of the benthos. Some species may be active and able to avoid the grab, while others burrow deeply and escape it. As the depth to which the grab digs depends on the firmness of the deposit, samples from different deposits may not be comparable. The present work, however, is concerned with the food of flatfish, and for this the sampling method appears to be adequate, since the fish examined were feeding almost entirely on the infauna in the top few centimetres of the deposit or upon slow-moving animals of the epifauna, all of which occurred in the grab samples.

Another problem of serious consequence for this work is that of the validity of the mean for a series of samples. There are usually fairly wide variations in the numbers of certain species throughout any series, suggesting that they are not evenly distributed on the ground. Nevertheless, the fairly close agreement between the means for adjacent stations on similar deposits supports the assumption that the means are a true measure of the population. Total numbers of organisms and total weights and in many cases numbers of single species expressed as percentages of the total animals present agree fairly well between the adjacent Stations 52 and 53, 50 and 55, 49 and 56 (Table 4), i.e. pairs in which the sampled areas are probably at about the same points in the gradient towards increasing silt content of the deposit.

In the case of *Amphiura*, which because of its abundance is the most suitable animal for statistical analysis, the validity of the means is borne out by analysis of variance, using the numbers occurring in each bottom sample (shown in Table 6).

Table 6. *Numbers of* Amphiura *in each bottom-sample, 23 May 1950*

Bottom ...	Fine sand			Muddy sand				
Station ...	52	53	51	54	50	55	49	56
Sample 1	·	1	1	1	31	87	118	143
2	2	1	·	69	39	91	110	147
3	·	2	1	16	95	86	86	85
4	·	1	·	36	94	21	137	152
5	1	1	1	45	86	83	123	69
6	1	1	1	70	69	47	133	130
7	1	1	1	44	43	71	129	114
8	·	4	1	74	89	75	114	106
9	·	2	·	83	74	85	90	126
10	·	1	·	44	119	67	66	116
Station total	5	15	6	482	739	713	1106	1188

It is unnecessary to include the three fine sand stations, 51, 52 and 53, in the analysis, since there is obviously a significant difference between the populations on fine and muddy sand. For the muddy sand stations results are as follows:

Stations	*F*	
54, 50, 55, 49, 56	13·38**	1% point = 3·77
54, 55	4·54*	5% point = 4·41
50, 55	0·053	5% point = 4·41
49, 50	10·04**	1% point = 8·28
49, 56	0·549	5% point = 4·41
55, 56	18·76**	1% point = 8·28

(* = significant; ** = highly significant)

There is therefore a significant difference between adjacent stations in a south-east to north-west direction, where the means show considerable differences, and no significant difference in a south-west to north-east direction, where the station means approximate to one another. Since *Amphiura* is absent from the mud ground, it seems probable that the numbers increase towards an optimum amount of silt in the deposit, although it is not certain that the amount of silt is in itself the controlling factor.

(*b*) *Analyses of gut contents*

Hynes (1950) discusses various methods of analysing data on the food of fishes based on occurrence, number, dominance, volume or weight, fullness, and 'points'. He shows that all give substantially similar results for the main components of the food. Hynes considers the 'points' method most satisfactory (the food items in each stomach were listed as common, frequent, etc., on the basis of rough counts and judgment by eye, due account being taken of the size of organisms as well as of their abundance. Each category was then allotted a number of points and all the points gained by each food item were summed and scaled down to percentages, to give the percentage composition of the food of all the fish examined. In allotting the points the size of the fish and the fullness of the stomach were also taken into account.) He argues in favour of this method that it is rapid and easy, requires no special apparatus, is not influenced by the frequent occurrence of a small organism in larger numbers, nor of heavy bodies, and does not involve trying to count large numbers of small and broken organisms. Against the method he mentions that it is subjective, but that this applies to all other methods, and that results given by the points method cannot be used for comparison with counts of the organisms in the habitat, though the last objection could be overcome by using a similar method in assessing the fauna.

It seems to me that for a small fresh-water fish such as the stickleback the points method is the most satisfactory, but that in the present work the number method is more accurate. With practice and a good knowledge of the fauna food organisms can be counted fairly rapidly and identified with certainty in the case of a marine flatfish of a minimum size of 15 cm. The food is seldom too much digested for identification and very small animals are not eaten. While it is necessary to estimate the numbers of some organisms which are broken up in passing through the gut, such estimation is at least as accurate as that inherent in the points method. In assessing the fauna, the weight of each species within its useful size-range expressed as a percentage of the total probably gives the best idea of its value as food, though it is also necessary to know the ratio of digestible to indigestible matter, but gut contents cannot be weighed accurately. The method of 'weighting' food organisms adopted by Ricker (1937) is dependent on counts for estimation of the total weight, and if the counts are inaccurate it follows that the weights are also in error. Since numbers were used for analysing the fauna off the Cumberland coast, for purposes of comparison it was essential to use numbers in estimating the food of the flatfish.

(*c*) *Feeding habits of the fish*

Comparison of the food of the three species of flatfish examined reflects the differences in feeding habit as described by Steven (1930). Plaice and dabs are both

visual feeders. Dabs are more active than plaice and take a wider range of organisms. Soles, on the other hand, are tactile feeders and are almost independent of vision for the finding and recognition of their food. The hunting posture of the plaice is more nearly horizontal than that of the dab, and its range of food approaches that of the sole. These differences are illustrated by the comparative utilization of the burrowing amphipod *Ampelisca*, which is difficult to see when in its burrow and is presumably discovered by touch or smell. The dab takes least, the sole most, and the plaice an intermediate number. Burrowing polychaetes are taken by the plaice to a greater extent than by the dab, while the dab captures more of the epifauna, such as *Aphrodite*, *Eupagurus* and *Philine*.

Todd (1915) recorded the gut contents of 4689 plaice from the North Sea. He states that there is a well-marked difference in the food of plaice in the winter compared with the summer. From November to February feeding is at a minimum and a high proportion of empty guts are found. In winter the food of those plaice that are feeding consists principally of Polychaeta, whereas in the summer Mollusca are the more important. He thinks that the change in food is not to be put down so much to a change in the comparative abundance of the food groups as to a voluntary change in the diet of the plaice. That the bottom fauna does not change much from season to season is the conclusion of most workers. Steven (1930) states that there is little change in the infauna as a whole over the year on the grounds he sampled off Plymouth. Blegvad (1928) states that autumn investigations in the Limfjord reveal as a rule a greater quantity of plaice food than do those in the spring, but considers this fact due to the special conditions in the fjord. No conclusions concerning seasonal changes in food can be drawn from the present investigations, but the difference in food eaten on the two different grounds within a short distance of each other shows that care must be taken in drawing conclusions unless the bottom fauna on the ground from which the fish were taken is known. Hertling (1928) and Blegvad (1930) show how the food of flatfish varies from one bottom community area to another.

Table 7. *The percentage occurrence of Mollusca and Polychaeta in plaice guts for each month (Todd's data)*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Empty	118	149	49	7	9	10	4	12	45	12	186	81
Mollusca	6·5	20·5	56·6	88·0	85·3	84·6	74·3	49·3	54·6	84·8	1·0	3·6
Polychaeta	17·0	32·0	51·5	38·5	24·3	48·0	34·1	39·7	30·4	30·4	1·0	13·4
Total guts	154	259	716	408	436	719	471	408	553	250	203	112

It must be pointed out that Todd's (1915) presentation of data on the seasonal change in food is rather misleading. In table A (p. 18) he lists the percentage occurrence of each phylum in the food of all plaice examined for each month, but the percentages are calculated only on guts containing food. Since the number of fish feeding is much lower in winter than in summer a false impression is gained from this table of the relative importance of Mollusca and Polychaeta at different seasons. Table 7 shows the percentages for these two groups for all fish observed by Todd, both full and empty.

It is evident that there is a reversal in the relative importance of Mollusca and Polychaeta, judged by occurrence, from summer to winter, but that from November

to January the amount eaten is much smaller for both groups than at other times of year. It is not possible to state with certainty that this reversal is not due to the movement of the general plaice population in winter on to grounds where Polychaeta are more numerous than Mollusca. On one ground at least—the Smith's Knoll Deep—Todd reported that Polychaeta formed a higher percentage of the food than Mollusca throughout the year.

In Table 5 the times of commencing each haul are shown. Each was of $1\frac{1}{2}$ hours duration. For comparable size-groups it can be seen that fish caught earlier in the day contain less food organisms per gut than those caught later. For plaice over 25 cm. caught near Station 51 between 0550 and 0720 hr., the mean number of food animals per gut was nine, and nearly all of these were in stomachs and hind-guts, the mid-guts being empty. Plaice over 25 cm. caught near Station 54 between 0745 and 0915 hr., contained an average of twelve organisms per gut and the hind-guts were usually empty, but food had reached the mid-gut. Fish of the same size-group caught near Station 55 between 0930 and 1100 hr., contained an average of fifteen organisms per gut, and the whole of the gut usually contained food. For the same size-groups caught near Station 50 between 1345 and 1515 hr., near Station 52 between 1620 and 1750 hr., and near Station 53 between 1830 and 2000 hr., the mean numbers per gut were respectively 24, 26 and 28, and in all cases the whole length of the gut contained food. These facts confirm the statement of Steven (1930) that plaice are visual feeders. Blegvad (1917) mentions that in the Limfjord plaice would seem to feed only during the day, and quotes some investigations of Petersen (1911) as to the contents of stomach and intestine of plaice at different times of day and night. These showed that as a rule fish were quite or almost entirely empty early in the morning, and full the whole day from 0800–1100 hr. to 2200 hr. It seems that plaice normally cease feeding after dark and commence again as soon as it is light enough to see their food, at least in shallow water. Whether they feed only by day in deeper water where the light intensity is low at all times is a matter for investigation. The lower intensity of light at the bottom in winter may have an additive effect to the lower temperature on the amount of food eaten. It further appears that food must be eliminated from the gut in less than 24 hours after eating.

There is no apparent change of any consequence in the kind of food eaten by plaice over the size range sampled in the investigation. The larger fish, as would be expected, contain more food than the smaller in the same haul.

Table 4 shows the extent to which the fauna is utilized by the plaice. The lower part includes species found in the bottom samples which did not occur in the fish guts. Of these some are probably of too rare occurrence in the fauna to appear in the food, including possibly *Sigalion mathildae* and *Upogebia deltaura*. Others are occasionally eaten, but were not identified in the guts of plaice collected during May 1950, including Nemertine sp., *Harmothoë* spp., *Sthenelais limicola*, *Glycera* sp., *Lumbriconereis* sp., *Priapulus caudatus*, *Venus striatula*, *Cardium echinatum* (foot), *Aloidis gibba*, and *Buccinum undatum* (syphon). Certain species are either too small or too large to be taken by adult plaice. In the former category are probably *Magelona papillicornis*, *Streblosoma bairdi*, most of the Cumacea and Amphipoda, *Thyasira flexuosa* and *Tellina fabula* on this ground; and in the latter when adult, *Anemone* sp.,

Hyas coarctatus, *Mactra corallina*, *Natica montagui*, *Asterias rubens*, *Astropecten irregularis*, *Ophiura texturata* and *Echinocardium cordatum*. Some of the large forms are otherwise unsuitable as food owing to their hard skeletal parts, shells or tubes, and the following are probably excluded for this reason, though of suitable size: *Onuphis conchylega*, *Phascolion strombi*, *Eupagurus bernhardus*, *Turritella communis* and *Natica poliana*. Unlike dabs, plaice seem to lack the ability to extract hermit crabs from their protecting shells. *Phascolosoma procerum* and smaller individuals of *Gonoplax rhomboides* are both eaten by dabs, and Steven found a single specimen of *Gonoplax* in a plaice. *Phascolosoma procerum* is sufficiently abundant on muddy sand to be readily available, and its absence from the plaice guts examined may be due either to chance or to selective feeding on the part of the fish.

(*d*) *Availability and selection of food*

Comparison of Tables 4 and 5 reveals that plaice almost certainly select their food. There is quite a good correlation between the fauna present and its appearance in the guts of the fish within suitable limits of size and availability. For example, *Ensis ensis*, which only occurs in the fine sand, is present in fish caught near Stations 51, 52, 53 and 54 and south-east of Station 50, i.e. near stations where fine sand deposits are present or adjacent. *Nucula turgida* is abundant in fine sand but occurs in very small numbers in muddy sand. It is absent from the guts of fish caught on muddy sand. *Cultellus pellucidus* has a wider distribution than *Ensis*, and occurs at some of the muddy sand stations, where it is eaten largely by the plaice. It is absent, however, from the faunal samples from Station 49 and only two specimens were found in fish from this station. *Amphiura filiformis*, on the other hand, is much more abundant in muddy sand than in fine sand, and is present to any extent only in plaice caught near stations on muddy sand. Similarly with *Pectinaria* spp. The occurrence of *Terebellides stroemi* in fish caught near Stations 51 and 52 may probably be explained by movement from the adjacent fine gravel and muddy sand in which the polychaete is present. Only one specimen was found from each station among sixty guts. Judging only from occurrence these facts would appear to favour the hypothesis that the plaice eat whatever presents itself of the available fauna. The facts certainly indicate that the fish do not move very far in search of food during the time that ingested animals remain in their guts. However, if numbers are considered it can be seen that the fish must actively select the animals they prefer—perhaps those that possess most food value. The numbers of *Cultellus* at Stations 50 and 55 were found to average 27 and 125 per m.^{2} respectively. The corresponding numbers of *Amphiura* were 739 and 713. Assuming that the two organisms are equally available the fish should eat many more *Amphiura* than *Cultellus* if they feed at random. From north of Station 50, however, twenty guts contained 133 *Cultellus* and 87 *Amphiura*, and from near Station 55, twenty-six guts contained 271 *Cultellus* and 14 *Amphiura*. What is known of the habits of the two species does not suggest that *Amphiura* is less accessible to the fish than *Cultellus*. Blegvad (1926) states that fish often bite off the arms of *Amphiura*, which wave in the water, leaving the disk which is concealed in the deposit. *Cultellus* also burrows with the head end of the shell protruding. *Amphiura* occurred in all samples from both stations and *Cultellus* in eight out of ten at Station 50

and nine out of ten at Station 55, so that both are presumably widely distributed on the ground; also the larger number of *Amphiura* (193) in twenty guts from near Station 49, where *Cultellus* is absent from the fauna, shows that the ophiuroid is readily available and will be eaten by plaice in some quantity when more attractive food is not present. It is therefore evident that plaice select *Cultellus* from among the available fauna in preference to *Amphiura*.

The questions of availability and selection have been discussed by several authors. Elton (1927) points out that there are definite upper and lower limits to the size of food an animal can eat, and this is discussed by Steven, who states that, apart from size, the availability of any animal for food will depend upon: (1) the habits and activity of the organism itself; (2) the habits and activity of the fish.

Allen (1941) states that both the behaviour of the fish and the nature of the animal under consideration may affect the extent to which it is eaten. Among the characteristics of a potential food animal which may have this effect are its size, appearance, habits and taste. The effect of the nature of the potential food animal on the extent to which it is eaten is the sum of these and other similar factors. It is this combined effect which may be termed the availability of the animal concerned.

These statements cover much the same ground, and their content is fairly obvious. Allen, however, is concerned to develop methods of measuring availability and extent of selection. He considers that it is not possible to measure the absolute availability of a food animal, but by comparison of fauna and stomach contents it is possible to compare the availabilities of different food animals. The most convenient comparison is that between the average percentage which the animal under consideration makes up of the stomach contents of a collection of fish and its percentage in the corresponding fauna. This ratio he terms the 'availability factor'. Larsen (1936) had previously used percentage weights in the reverse ratio to show the utilization of the fauna by various fishes in the Dybsø Fjord. Allen shows that in relation to the young salmon that he investigated it is possible to divide food animals into categories according to their availability factors which correspond closely with their habits when the latter are known. Similarly, Neill (1938) points out the relation between the relative accessibility of the different species in the fauna and the amount eaten by brown trout.

Allen further attempts to show that the young salmon select their food, and comes to the conclusion that fish containing only a few organisms are feeding at random, but that as the number of animals in the stomach rises the tendency to select increases. Unfortunately his conclusions are vitiated by an error in his manipulation of the data. He compares the stomach contents of the fish with what he calls the 'available fauna'. This quantity is calculated by multiplying the percentage made up by each animal or group of animals in the fauna by the corresponding availability factor, and then reducing the results to a percentage. But this in fact is a back-calculation resulting in the percentage composition of the food. Let a be the percentage of an animal in the food and b its percentage in the fauna. The availability factor for that animal is a/b. The 'available fauna' is then $b \times a/b = a$. Allen is thus comparing the stomach contents of the fish with the average composition of the food, and from this it is not possible to test whether selection takes place or not.

It is evident that the average composition of the fauna as it stands provides no guide to its availability as food for fish. If, however, the fauna is compared with the gut contents of a collection of the fish concerned taken from the same place, and the percentage composition calculated only from those species that are eaten by the fish, the results will be a measure of the available fauna for that species of fish on that ground. It is still not possible to determine how available any species may be relative to another owing to such effects as accessibility, conspicuousness, or activity, and any excess of an organism in the food contents of a fish over its occurrence in the fauna may be due to a combination of these effects rather than to selection on the part of the fish. It is obviously this difficulty which caused Allen to seek some other criterion of availability. Nevertheless, these effects cannot be estimated except in a general way, so that it is necessary to ignore them, and to treat that part of the fauna which is eaten by the fish as the available fauna. If the ratio, which I propose to call the 'apparent selection factor', of the percentage of an animal in the available fauna as defined in this way to its percentage in the food is calculated, the resulting figure will be a measure of its apparent selection by the fish. The term 'forage ratio' as used by Hess & Swartz (1941) is probably more appropriate for the availability factor as it includes the effects of selection as well as of real availability. To estimate the value of a fauna to a fish it is not necessary to distinguish between the two effects. It must be pointed out that such properties as taste and amount of indigestible matter in an animal cannot affect availability apart from selection, for if they reduce the apparent availability it must be because the fish avoid eating the animal where more attractive food is present.

For plaice feeding on the infauna of the surface layer of a soft deposit there is not much reason to suppose that any species is much less accessible than another, and it is reasonable to presume that the fish select certain species. If this is so an 'apparent selection factor' of more than unity will indicate that the fish select that species in preference to the general fauna, and the higher the factor the greater the preference. On the other hand, Neill and Allen show that accessibility is probably more important than selection by fish that feed by sight in such an environment as a rapidly flowing stream, where potential food species may habitually live by day under the shelter of stones and so be relatively inaccessible.

Table 8 shows the 'apparent selection factors' for the plaice caught off the Cumberland coast in May 1950. It can be seen that on fine sand plaice prefer *Cultellus* and *Ensis* which together make up more than 97% of the food by number, while *Ampelisca* is eaten more or less at random. Other animals, though making up 69% of the available fauna, are rarely eaten. On muddy sand *Cultellus* is still preferred to any other species, but although it is evidently sought still more than on fine sand, and makes up 72% of the food, its smaller numbers (3·9% of the available fauna) compel the fish to eat other animals in greater quantity, and to make up the deficit certain other species are selected to a lesser extent. *Amphiura*, although still avoided when other food can be obtained, is so preponderant in the fauna that it makes up 18% of the food.

Table 8. *The 'apparent selection factors' for plaice caught off the Cumberland coast, May* 1950

$$\text{Apparent selection factor} = \frac{\%\text{ by number of animals in food}}{\%\text{ of animals eaten in fauna}}.$$

Station	52			53			51			54			South of 50			North of 50	55		49
Length of fish (cm.) ...	>25	20–25	<20	>25	20–25	<20	>25	<20	Mixed	>25	20–25	<20	>25	20–25	<20	Mixed	>25	20–25	Mixed
Aphrodite aculeata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1·68
Nephthys spp.	·	·	·	0·04	0·10	0·06	0·10	·	·	·	0·10	·	0·09	·	·	0·16	0·39	0·10	2·00
Goniada maculata	·	0·38	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Owenia fusiformis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1·61
Pectinaria spp.	·	·	·	·	·	·	·	·	·	·	0·16	·	0·32	·	·	2·05	·	·	3·91
Terebellides stroemi	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	31·60
Diastylis spp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1·01
Ampelisca spp.	·	·	·	0·96	·	0·62	0·69	1·15	0·34	0·53	1·95	·	1·24	0·41	0·30	2·96	5·51	1·29	7·26
Corystes cassivelaunus	0·50	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Nucula turgida	0·12	0·005	·	0·01	0·004	0·01	·	·	0·006	0·18	·	·	1·02	·	0·37	·	·	·	·
Mysella bidentata	·	·	·	·	·	·	·	·	·	·	·	·	0·21	·	·	·	·	·	1·47
Gari fervensis	·	·	·	·	·	·	·	·	·	·	·	·	0·95	·	·	·	·	·	·
Abra alba	1·51	·	·	·	·	·	·	·	·	·	·	·	1·08	·	·	·	1·69	0·42	·
A. prismatica	·	·	·	·	·	·	·	·	·	·	·	·	0·95	·	·	·	·	·	·
Cultellus pellucidus	3·29	4·21	4·59	4·62	4·76	4·64	2·95	3·00	2·98	11·40	10·50	11·50	29·40	34·30	33·70	17·80	5·88	7·69	·
Ensis ensis	5·44	3·36	1·70	1·65	1·40	1·63	1·43	1·39	1·54	44·80	46·10	48·00	·	·	·	·	·	·	·
Cylichna cylindracea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·11	·	·	0·27
Philine aperta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0·95	·	·	0·60
Amphiura filiformis	0·06	·	·	·	·	·	·	·	·	·	0·06	·	0·07	·	·	0·43	0·17	0·02	0·79

SUMMARY

1. In a small area near the Cumberland coast the bottom fauna was investigated mainly with a grab and compared with the gut contents of flatfish.

2. The bottom deposits consist of muddy sand over most of the area, grading into mud in deeper water, with a patch of fine sand extending into the south-eastern part and some rough ground along the north-eastern edge. The fauna of each ground is described.

3. The gut contents of the fish varied with the ground on which they were feeding. On fine sand both plaice and dabs fed chiefly on the lamellibranchs *Cultellus* and *Ensis*. On muddy sand *Cultellus* was still the chief food of plaice but the ophiuroid *Amphiura*, which was very abundant, was eaten where *Cultellus* was scarce, while dabs ate more *Amphiura* than *Cultellus* even where the latter was present in some quantity.

4. It is concluded that the grab samples gave a reliable estimate of the potential food animals at each of eight stations worked during May 1950.

5. Of the various methods of analysing the gut contents of fish it is thought that estimation of the numbers of each food species was most appropriate in this investigation.

6. Feeding habits of the fish are discussed, and further evidence is brought forward that plaice are visual feeders and therefore feed only by day. Possible reasons are suggested for rejection by the fish of certain animals in the fauna.

7. It is shown that plaice probably select certain species from among the available fauna.

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AN ADULT POPULATION STUDY OF *PYRRHOSOMA NYMPHULA* (SULZER): (ODONATA: COENAGRIONIDAE)

By PHILIP S. CORBET

Department of Zoology, University of Cambridge

(With 3 Figures in the Text)

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INTRODUCTION

Developments of methods for population analysis since 1930 have shown that much can be learned about animal ecology by marking and recapturing specimens. Lincoln (1930) suggested a formula for estimating population size by analysis of banding returns amongst wild duck; this has since been elaborated to allow for birth, death and movement. Borror (1948) and Bailey (1951) have reviewed progress in this field.

Success of recapture methods depends upon the sampled population being closed and isolated; in this respect, certain Odonata with feeble flight, notably Zygoptera, are especially amenable to study. These insects commonly occur in compact colonies, of relatively short adult duration and centred round an aquatic habitat, often of restricted area. Apart from the work of Borror (1934) on *Argia moesta* Hagen, they have received little attention despite an introductory review by Cowley (1938). Borror's work was mainly designed to study movement and colour changes during the life of individuals, which were distinguished by spots of indian ink on the wings. No serious attempt was made to study survival-rate, daily population size or longevity under natural conditions, although several approximate conclusions were reached.

To obtain quantitative information upon these aspects of adult life, an isolated colony of *Pyrrhosoma nymphula* (Sulzer) was studied by marking and releasing specimens throughout the flying season. Results showed that Zygoptera are suitable

for study by such methods and that considerable information can be obtained by their use. This work was carried out in the spring of 1951, when the population was observed from the time of emergence until the end of the flying season.

HABITAT

The habitat centred around a small, permanent pond near Reading, Berkshire. In spring this pond was about 80 yards long by 20 yards wide, but contracted in area considerably during summer. It represented the head of a small runnel arising from the top of a Tertiary clay plateau covered by a thin veneer of coarse plateau gravel. This headstream had been dammed at a point just below the first exposure of clay. The pond, therefore, lay half upon gravel and half upon clay and was surrounded by an acid gravel common. The unusual combination of substrata rendered it highly productive.

No vegetation overhung the water except in the region of the clay dam where *Quercus*, *Rubus* and *Salix* grew, the slope of the shores being for the most part very gradual. The whole pond could easily be circuited by paths or grassy clearings. The ground vegetation of the common was chiefly *Pteridium*, *Calluna* and *Erica*, liberally dissected by gravel paths and clearings. Young trees of *Betula* and *Pinus* formed a scattered scrub association with *Ulex* and *Cytisus* in more exposed situations. There were a few old trees of *Quercus*, *Pinus* and *Betula*.

The habitat was ideally suited for collecting adults of *Pyrrhosoma*. These were abundant on and around clumps of *Pteridium*, *Rubus* and *Ulex* and often lower branches of *Betula*, where these were exposed to the sunlight. Individuals flying over the water were usually concerned with oviposition and commonly came to rest on low vegetation on the banks or dam and often on the light-coloured clay path; they were consequently not difficult to capture. Collecting was carried out in a belt about 20 yards wide around the pond. This represented quite a small part of the area over which the colony dispersed, but in such a localized population the aquatic habitat forms the most important reproductive region and must be visited often and regularly by all the individuals. Activity of this species was sufficient to secure adequate randomization within 24 hr. after release. Adults recaptured soon after release on the same day had spread rapidly from the point of release, and had become widely distributed. It thus provided a suitable and effective sampling area. Only one other suitable breeding site for this species lay within a mile of the habitat: this was surrounded by dense woodland. *Pyrrhosoma* bred in this pond but no specimens marked in the sampling area were found in samples taken there. There is no reason to suppose that migration occurs in this species; Borror (1934), studying *Argia*, found that adults moved only short distances, and at no great speed.

EMERGENCE

Study of emergence, both by direct observation and by collection of exuviae, was facilitated in 1951 by the late fall in water-level, which greatly restricted the number of plants available for use as supports by emerging larvae. Collections of exuviae were only made from upright, aerial plants (mostly *Juncus*) growing near the shore with submerged roots. These collections were necessarily incomplete: exuviae of

this species are small and cryptic and many larvae crawled some distance from the pond to emerge, their exuviae being lost.

The main emergence was restricted to the period 20–28 May. It was not observed outside this period, but adult captures indicate that small numbers continued to emerge until the beginning of July. On fine days emergence showed a well-marked diurnal periodicity, liable to modification by variable weather conditions involving morning rain. The first larvae began to leave the water at about 8.30 a.m. (B.S.T.), and the daily peak usually lay between 9.00 and 10.00 a.m. when larvae could be seen swimming actively towards the shore near the surface. They appeared to test upright plant stems for stability, often climbing several inches up the support only to flick themselves off into the water to try again elsewhere. Often larvae reached the shore before a satisfactory support was found; then they left the water and wandered amongst grass tussocks searching for suitable sites. Many continued some distance from the water's edge; others emerged immediately upon landing.

Table 1. *Daily emergence peaks, shown by collections of exuviae, and their correlation with subsequent adult arrivals*

	Exuviae collected					Adult arrivals	
	Male	Female	South and east shores	West shore	Total	Corresponding arrival peak	Interval (days)
20 May	3	4	—	—	7	—	—
21	24	16	6	34	40	**3 June**	14
22	1	0	0	1	1	—	—
23	15	8	9	14	23	**7 June**	16
24	4	4	2	6	8	—	—
25	14	3	9	8	17	**11 June**	18
26	—	—	—	—	—	—	—
27	—	—	—	—	—	—	—
28	0	1	0	1	1	—	—
Total	61	36	27	63	97	—	—

Soon after landing, one larva met a spider beneath a grass tussock. When the spider approached closely, however, the larva flexed its abdomen and caudal lamellae towards it with great suddenness, and the spider immediately withdrew. Such larval behaviour was not observed at any other time.

Most larvae only climb about half an inch above the water surface to emerge. After selecting a position, the abdomen is wriggled violently from side to side. This probably tests the grip of the legs and ensures that ample space exists for expansion of the wings. In a few minutes the thoracic cuticle splits and from 1 to 2 hr. later the teneral adult is ready for flight. It then climbs to the top of its support and flies shoreward, to alight upon a low bush or tree. The first flight seldom seems to exceed 20 ft.

As a rough quantitative estimate of the relative sizes of daily emergences, exuviae were collected daily from the zone of upright littoral plants mentioned above. The same regions were sampled each day and collecting was continued until a circuit of the pond revealed no more exuviae. The pond was approximately triangular in shape and, except on 20 May, collections from the three shores were recorded separately. Daily records of collections are shown in Table 1 and Fig. 2. There were three

distinct emergence peaks, on 21, 23 and 25 May. These probably represent a dispersed single peak, since weather conditions at the time of the daily mass emergence were unfavourable upon 22 and 24 May. On 22 May frequent heavy showers occurred in the morning and on 24 May, although fine weather followed, there was a violent thunderstorm from 8.00 to 8.45 a.m.

Far more adults emerged on the western shore than elsewhere, although supports were as plentiful on other shores. This was probably largely due to the western shore being sheltered from the prevailing wind; also, the eastern and southern shores were shaded from the sun until about 9.00 a.m., whereas the western shore received the first sunlight. However, the possibility remains that more larvae could have emerged on the land on eastern and southern shores since exuviae were only collected from the zone of littoral plants. Need for shelter from the wind could still have been responsible for the observed difference.

The proportion of male exuviae, 63%, is considerably higher than the value to be expected were the sexes emerging in equal numbers. The likelihood of this result being a chance deviation from equality is small ($P < 0{\cdot}02$) and it appears that males emerged in greater numbers than females in 1951. Only if females were more selective than males in their choice of emergence supports could such a result have arisen erroneously from a population having a sex ratio of unity. This seems unlikely; the sexes showed no preference for either shore, as might have been expected had differential choice of supports been a factor in the result. There is no evidence suggesting that either sex emerged first. The validity of this sex ratio will be discussed later under the appropriate heading.

FLYING SEASON

The flying season is here taken to mean the period between the appearance of the first mature adult insects at the pond, and the disappearance of the last. The first mature adult, a male, was seen at the pond on 30 May; several adults were flying on 31 May and the species was common for the first time on 1 June. The last adult was a male caught on 19 July, but the latest date is of little significance since protracted emergence of a few retarded individuals may greatly extend the flying season. An active population of adults existed at the pond from 1 June to 1 July. By 6 July almost all adults had disappeared.

There is a distinct gap between emergence and the beginning of the flying season, as shown in Fig. 2. This represents the time required for the maturation of teneral adults and is about 15 days in *Pyrrhosoma*, as will be discussed later. Borror (1934) found this period to be about 14 days in *Argia*.

POPULATION ANALYSIS

(*a*) *Methods of analysis*

The methods of analysis employed in this paper are described in detail by Fisher & Ford (1947). As Bailey (1951) has pointed out, no satisfactory method at present exists for determining the precision of population estimates made from large trellis diagrams of recapture data. This author evolved a simple maximum likelihood

equation suitable for catches taken on three occasions only, but this is not applicable in the present study in which information is required upon survival and daily population size throughout the flying season. Despite the handicap of being unable to express the accuracy of the results, Fisher & Ford's method of analysis has proved to be of great practical value for small populations and to yield much useful information at present unobtainable by any other means.

To apply Fisher & Ford's method, a value for a constant daily survival-rate is assumed which provides the least differences between observed and expected days survived by recaptured specimens. A survival rate giving the best fit allows the number of date-marks* expected in the population upon any date to be calculated. The number of marks captured and the total number of captures upon any date being known, Fisher & Ford showed that the population size upon a date d of capture can be calculated by use of the following formula:

$$\text{(Population upon } d\text{)} = \frac{\text{(Total number marks expected flying on } d\text{)} \times \text{(Total number individuals captured on } d\text{)}}{\text{(Total number marks recaptured on } d\text{)}}.$$

(*b*) *Sampling technique*

In the study of *Pyrrhosoma*, samples were taken within a belt of about 20 yards around the pond as often as weather would permit. One sample was caught upon each suitable day, specimens marked with a date-specific mark and immediately released from a point within the sampling area. Specimens were marked upon the body or wings with cellulose paint which was applied with a dissecting needle. Two brands of paint were found to be satisfactory: 'Aerocar' Brushing Cellulose Enamel (Valay Industries Product) and 'Brushing Belco' (Rawlplug Paint Company). Three colours were employed for the twenty-four date-marks needed. Dragonflies were marked at the bases of the legs, upon the thoracic episterna and upon dorsal and ventral surfaces of the abdominal segments. Hairiness of the thorax made it necessary for the paint to be applied in a dilute condition in order to grip the cuticle. Wings were marked at their bases and upon no occasion did subsequent flight appear impeded by increased load. Some insects were damaged during capture and specimens showing inability to fly normally upon release were killed and their deaths recorded. Fig. 1 shows that such cases were rare. This diagram gives the information concerning the daily numbers of captures, recaptures and releases. Dots in a date column indicate that no sample was taken upon the date in question. On all occasions until 6 July this was due to bad weather which rendered adults inactive, except for 2 June, when no sample was attempted. On 9, 13 and 19 June weather conditions were unfavourable but a few specimens were taken. Samples in July, however, were made on fine days, the small numbers of captures being due in this case to scarcity of adults. No adults were released after 3 July; therefore population analyses do not continue beyond 6 July, the first date of collection after 3 July. Numbers in small type beneath recapture records in the central squares in Fig. 1 are the calculated

* 'Date-marks' and not 'marked insects', since some individuals may have been caught and marked more than once.

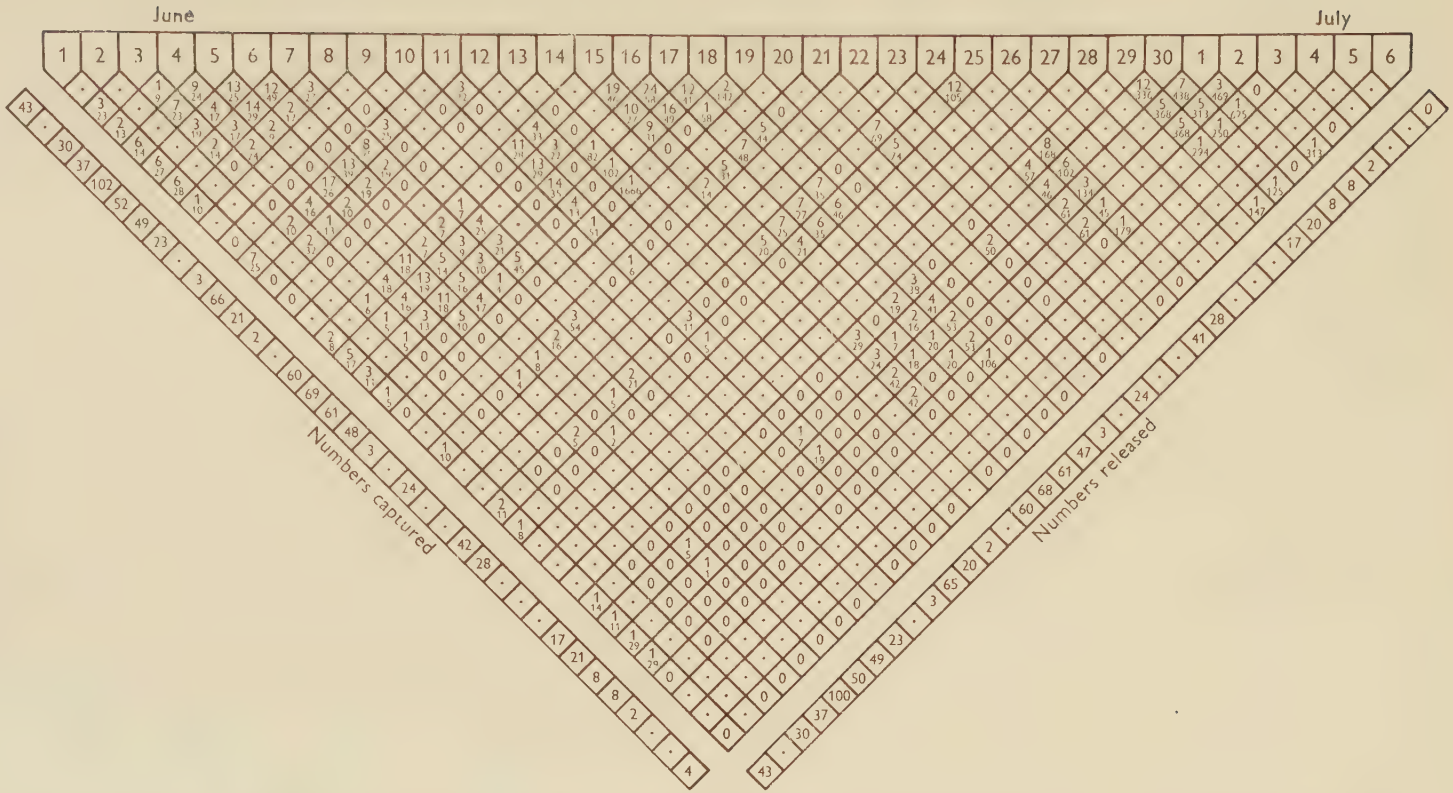

Fig. 1. Trellis diagram showing recapture data obtained during the flying season 1951. Large figures in the central squares give the observed recapture values, the small figures below them give the calculated relative recapture frequencies which would have been obtained had 100 specimens been captured and released on each occasion.

relative recapture frequencies, i.e. the number of recaptures which would have been obtained had 100 specimens been caught and 100 released upon each occasion of sampling. The greater the proportion of the population recaptured, the higher these values become. Towards the end of the sampling period the relative recapture frequencies became very high despite the small size of samples, indicating that the total size of the population was small. From inspection of these values alone it appears that the population sampled was large during the first fortnight in June, had grown smaller by 19 June, and had greatly diminished in size by 30 June. After this date adults gradually disappeared altogether.

(*c*) *Survival-rate*

Table 2, which is based on Fisher & Ford (1947), gives a calculation of differences between estimated and observed days survived by recaptured insects and assumes a constant daily survival-rate of 0·85. Higher and lower rates of survival were assumed and calculated: the total excess of observed over expected values assuming a constant daily survival-rate of 0·84 was 173·912; assuming a rate of 0·86 it was −124·822. Thus, 0·85 gives the best fit over the whole sampling period, the average value lying between 0·853 and 0·854. This corresponds with a daily elimination rate of about 15% and an expectation of life 6·67 days.

Although the given survival-rate provides the best fit for the whole flying season, the grouping of signs of the differences shows that it is consistently too low during the first half of the season and too high during the second. Overall accuracy of the survival-rate can be tested in another way. Since the approximate number of surviving insects marked at each previous date is known and also the number of recaptures, a distribution of frequencies of animals expected to be caught 1, 2, 3, ..., days after marking can be constructed. Expected values, assuming a daily survival-rate of 0·85, appear in Table 3. Total sums of observed and expected values lie very close, in view of the large range of class groups and the high frequencies involved. Inspection, however, of the series of differences indicates that observed values fall short of expectation for intervals from 1 to 10 days, exceed it from 10 to 20 days and show little difference for values greater than 20 days. These results are consistent with a survival-rate which decreases with age. Furthermore, the decrease of the survival-rate as the flying season progresses, as shown in Table 2, indicates that the population was fairly homogeneous with respect to the age of its members.

In view of the survival-rate changing with age, calculations of expected days survived were made for the first half of the flying season separately. For this, higher rates of survival were assumed. Table 4 shows a calculation of differences from 1 to 18 June assuming a survival-rate of 0·89 daily, a value which gives the best fit. Even so, almost the whole negative difference is provided by the expected value for 18 June. A calculation omitting this date, also in Table 4, shows an assumed survival-rate of 0·90 to give the best fit. Once again, the value for the last date gives the largest negative difference. It appears that the survival-rate is even higher than 0·90 from 1 to 16 June. It is clear that better agreement between observed and expected days survived could be obtained by assuming a regularly changing survival-rate, but besides being laborious, such a procedure would provide little further information.

Table 2. *Calculation of expected days survived by recaptures and daily population estimates assuming a constant daily survival-rate of 0·85*

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Dates of release	No. released	Time in days from date of release to 6 July	No. of marks from given dates expected to be flying on 6 July	No. of marks from those previous dates and pected to be flying on 6 July	Values in col. V weighted with days survived by marks	Total recaptures on dates in col. XII	Observed days survived by recaptures	Excess of observed over expected days survived	Total captures on dates in col. XII	Estimated total population on dates in col. XII	Dates of capture in June and July
5 July	—	1	—	48·2571	571·9814	3	17	−18·556	4	64·3	6
4	—	2	—	48·2571	523·7243	—	—	—	—	—	5
3	2	3	1·2282	48·2571	475·4672	—	—	—	—	—	4
2	8	4	4·1752	47·0289	427·2101	5	32	−13·420	2	30·6	3
1	8	5	3·5488	42·8537	380·1812	22	159	−36·184	8	29·9	2
30 June	20	6	7·5400	39·3049	337·3275	26	212	−11·140	8	27·3	1
29	17	7	5·4468	31·7649	298·0226	37	290	−57·134	21	47·8	30
28	—	8	—	26·3181	266·2577	21	179	−33·457	17	66·5	29
27	—	9	—	26·3181	239·9396	—	—	—	—	—	28
26	—	10	—	26·3181	213·6215	—	—	—	—	—	27
25	28	11	4·6788	26·3181	187·3034	—	—	—	—	—	26
24	41	12	5·8220	21·6393	160·9853	36	215	−52·804	28	100·7	25
23	—	13	—	15·8173	139·3460	43	385	6·170	42	108·8	24
22	—	14	—	15·8173	123·5287	—	—	—	—	—	23
21	24	15	2·0904	15·8173	107·7114	—	—	—	—	—	22
20	—	16	—	13·7269	91·8941	28	208	19·568	24	135·1	21
19	3	17	0·1887	13·7269	78·1672	—	—	—	—	—	20
18	47	18	2·5098	13·5382	64·4403	5	18	−5·800	3	129·1	19
17	61	19	2·7633	11·0284	50·9021	58	295	27·272	48	171·0	18
16	68	20	2·6180	8·2651	39·8737	78	457	80·728	61	142·7	17
15	60	21	1·9620	5·6471	31·6086	70	484	92·210	69	144·7	16
14	—	22	—	3·6851	25·9615	38	291	23·290	60	178·0	15
13	2	23	0·0470	3·6851	22·2764	—	—	—	—	—	14
12	20	24	0·3980	3·6381	18·5913	0	0	—	2	—	13
11	65	25	1·0985	3·2401	14·9532	12	65	9·260	21	285·0	12
10	3	26	0·0429	2·1416	11·7131	54	322	26·674	66	154·9	11
9	—	27	—	2·0987	9·5715	0	0	—	3	—	10
8	23	28	0·2346	2·0987	7·4728	—	—	—	—	—	9
7	49	29	0·4214	1·8641	5·3741	10	28	−0·829	23	420·4	8
6	50	30	0·3650	1·4427	3·5100	37	93	2·979	49	222·2	7
5	100	31	0·6200	1·0777	2·0673	26	60	10·132	52	295·3	6
4	37	32	0·1924	0·4577	0·9896	22	47	−0·564	102	342·4	5
3	30	33	0·1320	0·2653	0·5319	3	7	0·986	37	629·3	4
2	—	34	—	0·1333	0·2666	3	6	0·000	30	303·0	3
1	43	35	0·1333	0·1333	0·1333	—	—	—	—	—	2
								69·741			

Table 3. *Distribution of observed and expected intervals between marking and recapture assuming a constant daily survival-rate of* 0·85

Days	Expected	Observed	Difference
1	130·465	132	1·535
2	74·389	68	−6·389
3	49·720	44	−5·720
4	54·280	55	0·720
5	49·584	50	0·416
6	55·702	57	1·298
7	35·321	29	−6·321
8	29·318	26	−3·318
9	25·726	21	−4·726
10	27·392	32	4·608
11	20·048	26	5·952
12	19·193	26	6·807
13	18·450	19	0·550
14	14·741	15	0·259
15	9·289	12	2·711
16	6·363	8	1·637
17	4·440	4	−0·440
18	2·874	0	−2·874
19	4·164	4	−0·164
20	3·070	2	−1·070
21 and over	9·684	9	−0·684
Total	644·213	639	−5·213

Table 4. *Daily population estimates assuming constant daily survival-rates of* 0·89 *and* 0·90

	Survival-rate, 0·89		Survival-rate, 0·90	
	Days survived: excess over expectation	Estimated total population	Days survived: excess over expectation	Estimated total population
18 June	−33·512	219·3	—	—
17	−0·548	185·1	−19·382	197·9
16	16·340	195·1	12·480	210·0
15	2·808	256·4	−0·878	279·2
14	—	—	—	—
13	—	—	—	—
12	3·980	364·2	3·044	385·8
11	16·522	206·4	15·982	219·9
10	—	—	—	—
9	—	—	—	—
8	−2·280	489·3	−2·250	506·2
7	−1·387	251·2	−2·312	258·9
6	7·350	326·9	6·752	334·5
5	−2·522	387·9	−2·918	397·9
4	0·811	703·3	0·778	719·7
3	0·000	340·6	0·000	348·3
2	—	—	—	—
Total	+7·562		+11·296	

These analyses indicate that over the whole sampling period the average daily survival-rate was 0·85, involving an elimination-rate of 15% daily and an average expectation of life of 6·7 days. This survival-rate decreased with age. From 1 to 16 June it was more than 0·9 (10% elimination-rate with an expectation of life of 10 days), but up to 18 June it had fallen to 0·89 (11% elimination-rate with an expectation of life of 9·2 days). It decreased rapidly after that date to become considerably less than 0·85.

(*d*) *Daily population numbers*

Since daily population estimates depend upon assumption of the correct survival-rate, the most accurate estimates of daily population size for the period 1–17 June will be those assuming a survival-rate of 0·90 (Table 4). Similarly, an estimate for 18 June should assume a survival-rate of 0·89. For subsequent dates Table 2 may be used, but these estimates will be inflated because the survival-rate fell below the average value upon these dates. Estimates for daily population size from Tables 2 and 4 are plotted in Fig. 2. Values show great consistency after 12 June, but three distinct peaks appear before that date; these occur on 4, 8 and 12 June. Each peak is followed by a rapid fall in numbers. The possibility that each of these peaks represents an arrival of unmarked mature adults can be investigated further.

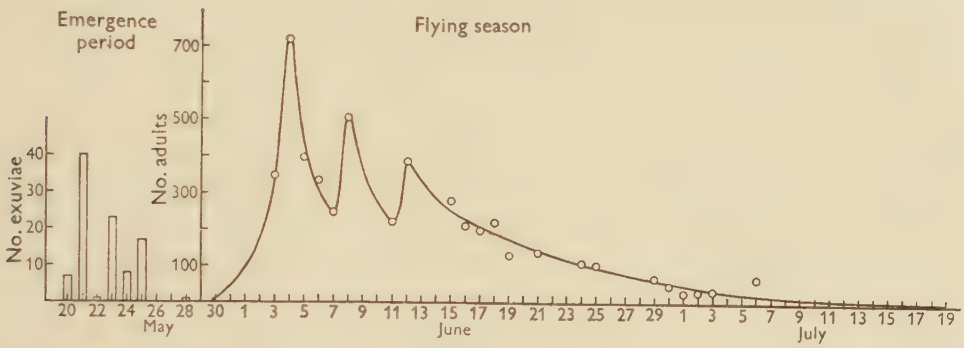

Fig. 2. The relationship between daily emergences and daily population numbers of mature adults. The three emergence peaks are followed by three groups of adults arriving at the population by the pond. An interval of about 15 days separates corresponding peaks of emergence and adult arrival.

Arrival of unmarked adults into a population containing a proportion of marked individuals will bring about dilution of marked forms. This will be associated with a sudden drop in frequencies of recaptures of insects marked before the influx. Dowdeswell, Fisher & Ford (1940) endeavoured to use this fall in recapture frequency to determine the location and magnitude of emergence. Ratios between recapture-frequencies (the sums of recaptures from previous dates divided by total captures) of successive dates were found and from these a series of numbers was constructed lying in the ratios successively observed. In the construction of these ratios, releases from the first compared date were not included in the sum of recaptures for the second.

The numbers obtained from these ratios provide an expression of relative abundance of marked specimens in the population on successive dates. Table 5 shows such a series calculated for recapture data for *Pyrrhosoma*. Sudden and considerable drops in the proportion of marked specimens (exceeding the general trend) occur between 3–4, 7–8 and 11–12 June. Averages of relative recapture values (the figures in small type in Fig. 1) for successive dates also show marked drops on 4, 8 and 12 June. These three methods are simply different ways of analysing the same information, but all support the view that there were three large arrivals of unmarked individuals into the population at the pond between 3–4, 7–8 and 11–12 June.

It seems probable that these three arrivals are correlated with the three emergence peaks occurring 2 weeks previously. Table 1 and Fig. 2 compare the intervals between peaks of emergence and adult arrival. Relative sizes of the peaks suggest that the association is a real one. Unfavourable weather conditions obtaining on 9 and 10 June would have increased the interval between the last peaks of emergence and arrival by delaying the appearance of adults. It seems reasonable to conclude that the period spent away from the water after emergence is about 15 days. This is consistent with Borror's findings for *Argia*.

Table 5. *Relative abundance of marked specimens on successive dates*

(Marked changes in the population are shown by heavy type)

	Recapture ratios between successive dates	Series showing relative abundance of marked specimens
3 June		2673
	1·8511	
4		**1444**
	0·6362	
5		2271
	0·8627	
6		2631
	0·9800	
7		2685
	2·4808	
8		**1082**
	0·5627	
11		1923
	1·9091	
12		**1008**
	1·0084	
15		1000
	0·8567	
16		1167
	1·1549	
17		1010
	1·3272	
18		762
	1·2083	
19		630
	1·4286	
21		461
	1·3611	
24		339
	1·1944	
25		283
	1·6813	
29		168
	1·0376	
30		162
	1·3480	
1 July		120
	1·3684	
2		88
	1·1000	
3		80

It is interesting to note that the pond population falls precipitously during the days immediately following an arrival. This drop is greatly in excess of the regular fall due to death observed after 12 June and may be due to dispersal away from the pond. Population pressure set up by arrival of an emergence group may stimulate dispersal away from the site of overcrowding. Probably adults showing the greatest tendency to leave the pond are those that were already flying before the arrival. This is suggested by the low values for subsequent average recapture frequencies for specimens marked and released on 3, 7 and 11 June. Had the new arrivals left, low recapture frequencies might have been expected for 4, 8 and 12 June. As it is, average recapture frequencies rise abruptly upon these dates, suggesting that new arrivals remain.

If these results provide an accurate expression of recapture trends, the reasonable conclusion may be reached that adults flying at the pond are gradually replaced by a series of successive emergence groups. Time of appearance of these groups is determined by the degree to which the mass emergence, 15 days previously, is split up by weather conditions prevailing in the morning. In 1951 the adult population of *Pyrrhosoma* appears to have been made up of three early batches of arrivals and

not regularly reinforced by a continuous succession of emergences. Under favourable weather conditions obtaining during emergence, maturation and adult arrival, concentration of these groups would be yet greater.

(*e*) *Longevity*

There are several ways in which an estimate of longevity can be made. An estimate of average expectation of life for the whole population during the flying season gave the value of 6·7 days (Table 2). Another method is to find frequencies of time intervals between marking and recapture. Observed values in Table 3, however, do not provide a true expression of longevity, since individual adults can be recorded in more than one class group. A better estimate is provided in Table 6. This gives the distribution of time intervals between first and last captures of the 233 individuals

Table 6. *Observed intervals between first and last captures of male and female individuals*

Days	Males	Females	Total
1	32	8	40
2	23	4	27
3	10	5	15
4	13	4	17
5	11	3	14
6	19	4	23
7	7	1	8
8	9	1	10
9	11	1	12
10	11	1	12
11	6	1	7
12	12	0	12
13	9	0	9
14	7	2	9
15	3	1	4
16	3	1	4
17	3	0	3
18	0	0	0
19	2	1	3
20	1	0	1
23	1	0	1
26	1	0	1
31	1	0	1
Totals	195	38	233

that were recaptured after release. In this table, for example, the male recaptured 31 days after first release is only recorded once, although captured six times within that period. A weakness inherent in this method is that the age of an individual is conjectural at the time of its first capture, but only the difficult procedure of exhaustive marking at the time of emergence could overcome this difficulty. The high proportion of recaptures suggests that the chances of an individual adult being captured were high; in this way the error would be greatly reduced, as it would also by sampling throughout the flying season.

The total average expectation of life from the series in Table 6, being the mean of the time intervals between first and last captures, is 6·76 days. This involves a daily survival-rate of 0·852 and a daily elimination-rate of about 15%. These results agree very closely with those obtained from Table 2, and substantially support the

assumption of these values during the flying season. Table 6 suggests that females may suffer a higher death-rate than males.

The values in Table 6, expressed as percentages of adults surviving after the maturation period, allow an incomplete survivorship curve to be drawn for adults during the flying season (Fig. 3). At present, no data exist concerning mortality in the first 15 days of adult life. Jackson (1948) found that survivorship curves for *Glossina* were similarly affected by inactivity of males during the first 2 weeks of adult life.

Adoption of values of 6·7 days for the average expectation of life, and 31 days for an approximation to the maximum life span appears to be sound. However, correlation of peaks of emergence with those of adult arrival shows a period of about 15 days to exist between them. Thus, values for survival-rate and longevity only apply to adults surviving this initial period of inactivity, and must be modified accordingly. For adults surviving the maturation period, it is safe to say that the

Fig. 3. Survivorship curve calculated from recapture data for mature adults surviving the initial maturation period of 15 days.

maximum life span is about (15 plus 31) days, or about 6½ weeks, but that the average expectation of life is only about (15 plus 6·7) days, or about 3 weeks. Borror (1934) stated that, for *Argia*, the maximum length of adult life is about 4 weeks, the average probably being about 3. Adults of *Pyrrhosoma* surviving to maturity in 1951 had an expectation of life of half the maximum life span. Values for survival probably vary considerably from year to year, as was found in *Panaxia* by Fisher & Ford (1947). The maximum adult life span forms a high proportion of the flying season, another indication of the homogeneity of the population with respect to the age of its members, caused by synchronization of early adult arrivals. In other species, of which the emergence curve was known, this principle could be used to obtain a rough estimate of the maximum life span.

(*f*) *Total numbers*

By summing daily population estimates and dividing the total by the average expectation of life, an estimate can be obtained of the total number of adults present during the flying season. To do this, population estimates must be extrapolated to provide for days upon which no samples were taken. From this it appears that the total population at the pond during the flying season lay in the region of 900; the total emergence probably exceeded 1000.

(*g*) *Sex ratio*

The 828 captures made during the flying season included 675 males and 153 females, there being 81·5% males. These captures involved only 421 individuals, 315 being males and 106 females, or 74·8% males. Owing to differential activity and habitat choice of the sexes, a high proportion of males is to be expected when sampling near the aquatic region of a habitat, even though the true sex ratio be unity. This has been discussed by Tillyard (1905), Tiensuu (1935) and Corbet (1951). The last

Table 7. *Daily population estimates of males, assuming constant daily survival-rates of* 0·90 *for* 1–17 *June, and* 0·85 *for* 18 *June–*3 *July*

Dates of capture	Observed days survived by male recaptures	Excess of observed over expected days survived	Total male captures	Estimated total population of males	Percentage males of total population
3 July	32	−14·315	2	20·8	67·7
2	156	−33·336	6	18·8	62·8
1	212	−17·138	7	18·9	69·5
30 June	288	−45·900	15	29·0	60·7
29	160	−33·819	13	45·7	68·8
28	—	—	—	—	—
27	—	—	—	—	—
26	—	—	—	—	—
25	214	−53·015	24	71·4	70·8
24	347	−5·264	31	73·5	67·6
23	—	—	—	—	—
22	—	—	—	—	—
21	199	25·892	20	100·7	74·6
20	—	—	—	—	—
19	9	−5·130	2	119·7	92·7
18	264	33·327	39	132·4	77·5
17	411	−21·784	51	149·5	75·5
16	473	4·283	63	157·5	75·0
15	277	−1·208	48	191·6	68·6
14	—	—	—	—	—
13	—	—	2	—	—
12	56	−0·815	15	246·7	64·0
11	293	17·768	56	170·3	77·5
10	—	—	2	—	—
9	—	—	—	—	—
8	25	−2·810	19	377·3	74·5
7	87	0·606	40	192·2	74·2
6	59	5·900	44	236·2	70·6
5	39	−4·567	77	296·3	74·5
4	7	0·466	33	530·6	73·7
3	6	0·000	22	231·6	66·5
					(av.) 71·8

two authors found the true sex ratio at the time of emergence for species of Anisoptera by collecting exuviae. Zygoptera are less amenable to this method of study and do not appear to have been used in this way hitherto. The only systematic work on a population of Zygoptera seems to be that of Borror (1934), who concluded from collections of adults that females were more than twice as abundant as males in *Argia*. This result is unexpected since the sexes appear to emerge in approximately equal numbers in several species of Anisoptera.

An attempt was made to determine whether the observed excess of males in *Pyrrhosoma* was based upon a real disparity, or was merely due to differential activity.

Recaptures of males and females were recorded separately; from these records survival-rates for both sexes can be found and daily population estimates made. Recapture frequencies of females being small in relation to total female captures and therefore subject to considerable error, these values have been calculated for males only. Table 7 shows estimated daily populations of males and the percentages that these represent of the total population upon each day. For 1–17 June a survival-rate of 0·9 was assumed, and for 18 June–6 July a rate of 0·85. Both values provided the best fit between observed and calculated values of days survived. The percentage values show great consistency and undergo little fluctuation except for 19 June, when the number of captures was very small. These estimates are independent of the numbers caught in each sample and are probably unaffected by differential activity. Consistency of these sex ratios indicates that there was indeed a real excess of males. Of the ninety-seven exuviae collected during emergence 63% were males, again a significant excess. In 1951 it can be assumed that males were about twice as abundant as females and composed about 70% of the total population. From this result it appears that the apparent numerical preponderance of males in the Odonata, although undoubtedly accentuated by differential activity, may sometimes be due to a real excess. It is extraordinary that previous work on the sex ratio in Odonata should have shown so little consistency. Males have been found to be about 30% of the total population in *Argia* (Borror 1934); about 50% in *Cordulegaster* and *Leucorrhinia* (Tiensuu 1935), *Anax* (Corbet 1951), and *Uropetala* (Wolfe 1952); and about 70% in *Pyrrhosoma*.

DISCUSSION

In temperate regions insects with aquatic larvae, having an adult life-span of less than a year, usually fly at restricted and well-defined periods of the season. By reducing interspecific competition in a limited habitat, and by synchronizing appearance of the reproductive stage, this is of adaptive value. Time of emergence is governed by the bionomics of the larval stage. In the Odonata, a group in which variation in growth-rates is notoriously wide, and in which duration of larval development may be from 1 to 3 or more years, one might expect restricted emergence to be an unusual phenomenon. Yet in *Anax imperator* Leach, a form emerging in spring, Corbet (1951) found emergence to be synchronized to such an extent that 94% of the yearly population of adults appeared within 14 days. Strong asymmetry of the emergence curve suggested that, at the last stage in larval development, an obligate resting stage intervened, allowing larvae in earlier stages to catch up with precocious members of their age-group. Were this resting stage long in relation to the temporal extent of variation, its completion would find almost the whole population equally prepared to respond to environmental factors stimulating metamorphosis.

In *A. imperator* Leach, it has recently been found* that most of an age-group enter the last larval instar in early autumn, between August and November. Upon entering the final instar, growth is prevented until the following spring. In this way natural variation in growth-rates is suppressed and nearly all of an age-group embark upon metamorphosis together, as soon as environmental conditions become suitable. Further uniformity is achieved by larvae selecting the same niche in early spring. The

* The observations supporting these conclusions will shortly be published.

maintenance of a life-history in which the final larval instar is entered in autumn is clearly of value to any spring-emerging species. From this, it might be expected that forms with a spring flying season would enter the last larval instar the previous autumn. This appears to be the case in three genera which have been studied: *Brachytron* (Münchberg 1931), *Anax* and *Pyrrhosoma*.*

A similar emergence curve may not exist in species emerging later in the season. In these forms, the last larval instar is probably entered shortly before emergence, growth being uninterrupted at this stage. In this way, variation in growth-rates would find expression in the emergence curve which would approach normality in form. This remains to be investigated. It is perhaps significant that species commonly observed to have a mass emergence (*Anax*, *Gomphus*) emerge in spring, whereas this phenomenon is seldom associated with species that emerge in summer. It may be then, that entering the final larval instar in autumn or spring is an important criterion of 'spring' or 'summer' species respectively, and it is possible that, in habitats unfavourable for growth, where entering the last instar is delayed until spring, a 'spring' species might exist as a 'summer' species in part of its range.

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SUMMARY

1. A localized population of *Pyrrhosoma nymphula* (Sulzer) was studied by marking and recapturing specimens during the flying season in 1951.

2. Emergence was restricted in time and showed a diurnal rhythm. Unfavourable weather conditions at the peak period between 9·0 and 10·0 a.m. (B.S.T.) postponed emergence until the following day. The mass emergence was thus divided into three day-groups. Shelter and warmth appear to be major factors influencing the choice of supports by transforming larvae. Collections of exuviae gave a sex ratio of 63% males.

3. The flying season, or period of mature adult flight, lasted from 30 May until 19 July, but an active population only existed at the pond from 1 June to 1 July.

4. Insects returned to the pond as mature adults about 15 days after emergence.

5. An average daily survival-rate of 0·85 gave the best fit with recapture data for the whole flying season. This involved a daily elimination-rate of about 15% and an average expectation of life of 6·7 days. The survival-rate fell from considerably more than 0·9 at the beginning of the flying season, to less than 0·85 at the end.

6. Daily population estimates show three main groups of adults to have arrived at the pond early in the flying season. These probably corresponded with the three emergence groups observed 2 weeks earlier. Numbers at the pond fell rapidly after arrival of an emergence group, new arrivals tending to replace the previous residents. The adult population was fairly homogeneous with respect to the age of its members.

* For note see previous page.

7. Adults surviving the maturation period had an average expectation of life of 21·7 days and a maximum life-span of 46 days. These values include the 15-day period of inactivity preceding mature adult flight.

8. The total number of mature adults at the pond was estimated at about 900. The total emergence probably exceeded 1000.

9. About 80% of total captures were males, a sex-ratio inflated by differential activity of the sexes. Analysis of recapture data showed about 70% males.

10. The effect of the larval life history in the Odonata upon the time and synchronization of emergence is discussed. It is suggested that species entering the final larval instar in autumn may be expected to have a mass emergence in spring.

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NOTE ADDED IN PROOF

Dr C. H. N. Jackson has drawn my attention to the error which results from combining recapture data for sexes showing differential activity when making estimates of total population size. Although the main conclusions in this paper are unaffected, sections (*f*) and (*g*) require modification. Figures in Table 2, Column XI, will be consistently too low, as will be the total estimates derived from them in section (*f*). In Table 7, male population estimates remain sound but the percentage values for males in the right-hand column probably provide expression of relative activity rather than real sex ratio. This prohibits the checking of the sex ratios derived from exuviae and individual captures by the method shown in Table 7. These modifications affect items 8 and 9 in the summary.

DIVISION OF LABOUR AND FORAGING IN *BOMBUS AGRORUM* FABRICIUS

By ANNE D. BRIAN
Feddens, Cardross, Dunbartonshire

(With 1 Figure in the Text)

INTRODUCTION

In a previous paper (Brian 1951*b*) the development of the brood of *Bombus agrorum* Fabricius in two observation nests was described. In these same nests (one in 1947 and the other in 1948) the behaviour of the individual workers was also studied. Each bee was removed from the nest on the day after emergence, weighed and given an individual mark with cellulose paints. The nests were watched for periods of 1 hr., twice a day in 1947 and once a day in 1948 and all entrances and exits of the foragers, together with the type of load brought in, were noted. In addition, a census of all bees present in the nest was made each day. Neither nest attained any great size or produced queens. This was due, in the 1947 nest, to the early substitution of the original queen by an invader who only laid drone eggs and was presumably unfertilized. Twenty-six workers and forty-three drones were produced in all. The 1948 nest produced forty workers and seven drones and the small size in this case can almost certainly be attributed to the very wet cold summer of that year. The small number of bees present in the nest at any one time was however an advantage since it facilitated accurate observation of individual behaviour. Two more colonies were taken for experimental purposes in 1949 and 1950 respectively both considerably larger than the 1947 and 1948 nests. All four of these colonies came from the same area in Dunbartonshire on the north bank of the Firth of Clyde.

DIVISION OF LABOUR

(*a*) *House-bees and foragers*

Both Pechards (1948) and Cumber (1949) have shown that in *B. agrorum* the workers found in a nest when it is dug up are on the average smaller than those caught returning from foraging, and thus, as they point out, confirms previous suggestions of a division of labour in the Bombidae according to size. This question has been further studied in the two observation nests where the day-to-day behaviour of the workers was recorded. It was found that, although on any one day this same division was apparent, during the whole life of each colony very few of the workers were never known to forage. The distinction between larger and smaller workers lay in the age at which foraging began and not in a clear-cut division of duties. This is shown in Tables 1 and 2 where the workers are arranged in order of weight. Although some small workers foraged early and some larger ones fairly late, there is an obvious tendency for the large ones to begin foraging about 5 days after emergence and the small ones 10 or more days later. This distinction is relative rather than absolute, as

Table 1. *Weight, age at first foraging and longevity of workers in the* 1947 *nest*

Bee no.*	Weight (mg.)	Age at first foraging (days)	Length of life (days)
10	220	4	28
16	200	8	9
22	190	6	27
9	180	5	37
11	180	5	15
20	170	4	47
13	160	7	20
12	160	7	21
15	160	6	51
3	150*	?	11+
21	150	3	14
17	140	6	22
8	140	?	14+
18	140	15	29
23	130	18	20
25	120	11	11
19	110	14	26
5	110	Never	23+
26	100	17	32
1	90†	?	64+
4	80	Never	23+
7	70	Never	19+
24	50	Never	45

* The bees are numbered in order of emergence (see Table 3).

† From first batch of workers, foraged for a few days after the nest was taken and then became a house-bee.

Table 2. *Weight, age at first foraging, and longevity of workers in the* 1948 *nest*

Weight (mg.)	Age at first foraging (days)	Length of life (days)
210	5	5
210	4	5
200	5	13
180	4	17
160	5	18
150	4	4
150	4	5
140	4	5
130	4	12
130	6	11
130*	?	69
120	?	21
120	5	38
110	6	21
110	?	20
100	7	7
100	8	12
100	28	37+
100	15	31
90	4	14
90	7	13
90	21	26+
80	36	36
60	Never	21
50	Never	37+
50	Never	18+

* From first batch of workers, foraged for a few days after the nest was taken and then became a house-bee.

on the average the 1948 bees were lighter than the 1947 bees and the division in 1948 falls around 100 mg. rather than around 140 mg. as in 1947. In Table 3 the daily foraging record for each bee in the 1947 nest is given. This shows that, having once begun, a worker would continue to forage regularly until it disappeared, presumably due to death (bees almost never died in the nest). Occasionally a break in the foraging sequence occurred; this usually meant that the worker was an abnormally long time on a foraging trip but sometimes a confirmed forager would, as it were, take a day off and remain in the nest. Two workers (nos. *15* and *22*) were exceptional in that after beginning to forage at an age normal for their weight they then remained in the nest for several days before resuming regular foraging. Two other workers (nos. *1* and *3*), both of the first batch, foraged for some days after the nest was taken and then were never seen to go out again. One of these (*3*) disappeared soon after, but the other attained a far greater age than any other worker in the nest. There was a similar anomalous worker in the 1948 nest; she, after foraging at first, remained in the nest for the rest of her very long life, but this will be discussed later.

Although never seen leaving the nest until they took to foraging, the non-foragers evidently made orientation flights at an early age, for if they happened to escape through the roof of the nest when the cover was lifted they could always find their way back by the correct entrance.

(*b*) *The change from house duties to foraging*

In the 1947 nest, owing to the early production of drones, an acute labour shortage developed towards the end of the season. From Table 3 it can be seen that the late changes from house-bee to forager (bees *23*, *25* and *26*) occurred about the time when the foragers on whom the colony had depended during late July and early August (bees *9*, *10*, *12*, *13*, *17* and *21*) were lost. It appeared that the smaller bees took to foraging in order to maintain the colony in the absence of other foragers.

If this were so it would mean that workers of *B. agrorum* could alter their behaviour to suit the needs of the colony, as has been shown to be the case in the honey-bee by Rösch (1930). In the honey-bee, however, the worker is only called upon to perform duties that she would carry out at some stage in her life in any case; either foraging at a slightly earlier age than normal, should old bees be in short supply or, if young bees are absent, reverting to jobs done at an earlier stage. But in the bumble-bee this adjustment to the needs of the colony would apparently require a complete switch from one set of duties to another set which, under different circumstances, might never have been performed.

Although changes from house duties to foraging at a late age were also observed in the 1948 nest, no conclusive evidence on their cause was obtained, and a third nest was collected in 1949 to test the matter. It was considered that if those bees that changed over from one job to another were responding to the needs of the colony the immediate stimulus must be, either shortage of food, or the lack of movement in the nest usually caused by the coming and going of foraging workers.

The 1949 colony was set up in the observation nest used previously, the workers measured (instead of weighed) and marked and the colony watched for hourly periods on 5 days from 26 July to 4 August to determine which workers were foraging and

Table 3. *Number of loads of nectar and pollen collected by bees in the* 1947 *nest from* 7 *July to* 31 *August*

Bee no.	Weight (mg.)	July																			
		7	8	9	10	11	12	13	14	15	16	17	18	24	25	26	27	28	29	30	31
Queen		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	90	3	3	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	100	1	2	1	0	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
3	150	8	0	1	0	0	0	0	0	0	0	0	0	·	·	·	·	·	·	·	·
4	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	·	·	·	·
5	110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	·	·	·	·
6	150	6	7	5	5	3	6	3	3	3	·	·	·	·	·	·	·	·	·	·	·
7	70	0	0	0	0	0	0	0	0	0	0	0	0	0	·	·	·	·	·	·	·
8	140	1	2	5	7	4	4	3	6	3	8	7	5	·	·	·	·	·	·	·	·
9	180	0	0	0	1	2	5	4	3	1	6	3	5	3	3	2	2	2	2	0	3
10	220	·	·	·	·	·	0	0	0	1	2	3	4	4	4	3	4	2	1	3	2
11	180	·	·	·	·	·	0	0	0	0	1	0	1	4	·	·	·	·	·	·	·
12	160	·	·	·	·	·	·	·	·	·	·	·	0	3	5	4	2	4	2	3	2
13	160	·	·	·	·	·	·	·	·	·	·	·	0	4	4	4	3	4	5	4	3
14	170	·	·	·	·	·	·	·	·	·	·	·	·	0	·	·	·	·	·	·	·
15	160	·	·	·	·	·	·	·	·	·	·	·	·	1	5	4	1	2	2	4	0
16	200	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	1	2	·	·	·
17	140	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	2	1	5	1
18	140	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	0	0	0
19	110	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	0	0	0
20	170	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	1	6	3	3	5
21	150	·	·	·	·	·	·	·	·	·	·	·	·	0	0	1	1	0	1	3	0
22	190	·	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	2	0
23	130	·	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	0	0
24	50	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	0
25	120	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0	0	0
26	100	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0	0	0	0

Bee no.	Weight (mg.)	August																					
		1	2	3	4	5	6	7	8	9	10	11	13	15	17	18	19	20	22	23	24	27	31
Queen		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1
1	90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	100	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
3	150	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
4	80	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
5	110	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
6	150	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
7	70	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
8	140	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
9	180	1	0	4	2	3	2	2	3	2	4	3	·	·	·	·	·	·	·	·	·	·	·
10	220	5	4	4	2	2	2	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
11	180	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
12	160	3	2	4	4	3	3	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
13	160	3	6	4	3	0	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
14	170	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
15	160	0	0	0	0	0	0	0	0	0	0	3	2	0	0	1	1	2	3	4	4	6	4
16	200	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
17	140	1	1	2	4	5	6	5	4	4	4	6	0	·	·	·	·	·	·	·	·	·	·
18	140	0	0	0	0	0	4	2	4	4	2	4	5	1	2	5	6	8	·	·	·	·	·
19	110	0	0	0	0	0	3	4	4	3	3	5	3	5	2	·	·	·	·	·	·	·	·
20	170	3	1	3	5	5	3	5	5	4	4	4	4	0	2	5	3	3	3	4	4	4	0
21	150	4	1	4	2	2	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
22	190	0	0	0	0	1	2	6	5	4	2	4	4	1	0	1	1	0	·	·	·	·	·
23	130	0	0	0	0	0	0	0	0	0	0	3	1	·	·	·	·	·	·	·	·	·	·
24	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	120	0	0	0	0	1	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
26	100	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	1	1	4	0	6	6	0

which were house-bees. The results are given in Table 4. After the watch from 9–10 a.m. on 4 August all foraging bees were caught and caged. The honey-pots of the nest were filled about half full with sugar syrup and this level was maintained so that there was never a shortage of 'nectar' for the house-bees. The nest was watched

Table 4. *Division of labour in the* 1949 Bombus agrorum *nest*

(H = bee in the nest; F = bee foraging during the observation hour.)

Bee, wing length (mm.)	July			August						
	26	29	30	4	10	12	14	16	19	22
12	H	H	·	·	·	·	·	·	·	·
11	F	F	F	F	F	F	F	·	·	·
	F	F	·	·	·	·	·	·	·	·
	F	F	F	F	F	F	F	F	F	·
	F	F	F	·	·	·	·	·	·	·
	F	F	F	F	F	·	·	·	·	·
	F	F	F	·	·	·	·	·	·	·
	H	H	H	H	H	H	H	H	H	H
	H	H	H	H	H	H	H	H	H	H
10	F	F	F	F	·	·	·	·	·	·
	F	F	F	F	F	·	·	·	·	·
	F	F	F	F	·	·	·	·	·	·
	H	H	H	H	H	H	H	H	H	H
	H	H	H	H	H	F	F	F	F	F
	H	H	H	H	H	H	H	H	H	H
	H	H	H	H	H	H	H	H	H	H
9	F	F	F	F	F	F	·	·	·	·
	F	F	F	F	·	·	·	·	·	·
	H	F	F	F	·	·	·	·	·	·
	H	H	H	H	H	F	F	F	F	F
	H	H	H	H	H	H	H	H	H	H
	H	H	H	H	H	H	H	F	F	F
	H	H	H	H	H	F	F	F	F	F
8	H	H	H	H	H	H	H	F	F	F
	H	H	H	H	H	F	F	F	F	F
	H	H	F	F	F	·	·	·	·	·
	H	H	H	H	F	·	·	·	·	·
	H	H	H	H	H	H	H	H	H	·
	H	H	H	H	H	F	F	F	F	·
7	H	H	H	·	·	·	·	·	·	·
6	H	H	H	H	H	H	H	H	H	H
5	H	H	H	H	H	H	H	H	H	H
Changes from H to F	·	1	1	0	1	5	0	2	0	0
Changes from F to H	·	0	0	0	0	0	0	0	0	0

for two hour periods and looked into at frequent intervals during the rest of the day. One bee which had previously always remained in the nest left, and returned with nectar once. On the following day the nest was again watched under weather conditions when foraging would normally have occurred but no workers went out. At 2.0 p.m. on that day (5 August) all syrup was removed from the nest and from then onwards the bees were looked at frequently. None of them made any attempt to leave the nest, and by the afternoon of 6 August were so weak they could barely move and, since obviously incapable of flight, would have starved to death if left alone. The foragers were therefore returned to the nest at 6.0 p.m. on 6 August and syrup given

to revive the house-bees, after which the colony appeared to proceed normally again. It was watched for hourly periods on six subsequent days up to 22 August and it can be seen from Table 4 that of the seventeen house-bees present in the nest at the time only one changed over to foraging in the course of the experiment, but seven changed subsequently and were therefore capable of foraging.

The first part of this experiment, removal of foragers while supplying syrup within the nest, was repeated with another colony in 1950. Almost the same result was obtained; no house-bees went out foraging. Unfortunately the weather then deteriorated to such an extent that no foraging could be expected under normal circumstances and the experiment was abandoned.

The conclusion drawn from these results is that the age at which a worker will start to forage has no connexion with the needs of the colony but is a constitutional, non-plastic character which varies from individual to individual and is associated with differences in weight. In practice this system, although more rigid than that operating in the perennial honey-bee colony, is well adapted to meet the needs of an annual colony in which all the workers are produced first and are followed by numbers of queens and drones which must be fed, but in the case of the drones, contribute nothing to the parent colony. The small house-bees, in addition to their nursing duties, may be regarded as a foraging reserve, which, in the normal course of events, will come into action about the time that the primary foragers become depleted through premature deaths and no young ones are available to replace them.

It is interesting to note that in the 1947 nest the queen herself resumed foraging at the end of the season.

(*c*) *Longevity of workers*

The age that the workers attained is shown in Tables 1 and 2. Unfortunately the whole life of a number of the house-bees was not observed, but it can be said that they tended to live slightly longer than the foragers. This was most noticeable in the 1948 nest when the short life of the foragers was attributed to the bad weather conditions with which they had to contend. Differential survival probably accounts for the fact that Cumber (1949) found a higher proportion of small bees in large nests. A survivorship curve has been drawn (Fig. 1) for the thirty-nine workers whose exact ages at death were known. This provides a good example of ecological longevity since the workers were not protected from natural hazards excepting those that would have led to destruction of the whole colony, such as damage by mice or trampling or severe starvation following bad weather. The curve is of the diagonal type with the death-rate roughly constant until old age. On the average, 29% of the bees died every 5 days (for the first 10 days the death-rate was lower). This implies that deaths were due to accidental causes; certainly very few were due to failure to orientate correctly since nearly all bees returned to the nest after their first day of foraging. The most likely cause of accidents in the field would be bad weather, notably wind. This is borne out by the fact that the foragers in 1948, a bad bee season, were not so long lived as those in 1947, a good season. The bumble bee has few predators in the field so that predation is not a likely cause of death.

Mortality in the brood stage in these two nests has already been described (Brian 1951*b*), in one 69% and in the other 64% of the eggs laid failed to produce adults.

(*d*) *The proportion of the population foraging*

One result of division of labour was that the foraging force always formed a fairly constant proportion of the total population of the colony: slightly less than two-thirds of the bees usually remained in the nest. This is shown as a frequency distribution in Table 5. Rösch (1925) found that on the average the honey-bee worker in summer spent 20 days on house duties and 10 days on foraging so that here, too, in a stationary population, about two-thirds of the bees would be present in the hive. But nursing duties, in particular larval feeding, are far less arduous in *B. agrorum* than in the

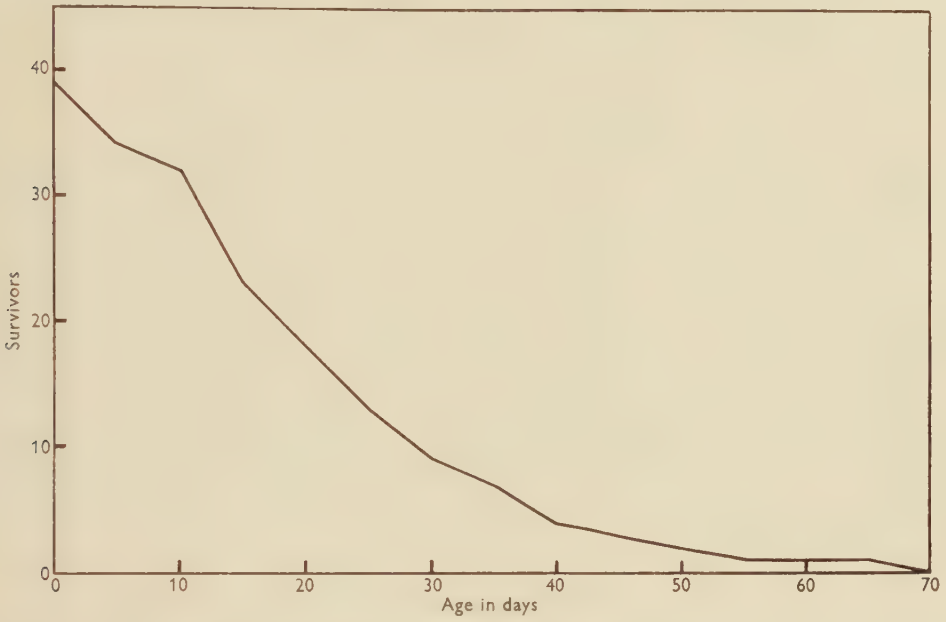

Fig. 1. Survivorship curve for *Bombus agrorum* workers.

Table 5. *Percentage of the total population foraging on each observation day*

		Percentage groups										Av.
		1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	
No. of days	1947	0	4	14	16	8	0	0	0	0	0	34
	1948	0	1	5	8	13	1	0	0	0	0	38
	1949	0	0	1	5	4	0	0	0	0	0	40
Total		0	5	20	29	25	1	0	0	0	0	

honey-bee. For example, Lineburg (1924, quoted by Wheeler 1928) records that each honey-bee larva receives, on an average, more than 1300 visits from the workers in 24 hr., but it was not unusual to watch a *B. agrorum* nest for an hour and see no larval feeding by house-bees at all, though more usually three or four larvae would be fed by one worker in that time. This is because in *B. agrorum* the larvae obtain the bulk of their food directly from the pollen placed in the pollen pockets by the foragers. Purposes other than larval feeding may therefore be served by the high proportion of bees that remain in the nest, in particular maintenance of temperature. Several

workers (Himmer 1933; Nielsen 1938) have shown that bumble-bees maintain the temperature of their nests above air temperature. In 1948 the temperature of the nest and the surrounding air was taken every day. The nest temperature ranged from 24 to 33° C. for air temperatures of 12 and 29° C. respectively, a difference of 12° C. at low air temperatures and 4° C. at high. These fluctuations are greater than those recorded by Himmer (1933) and Cumber (1949) for nests of *B. agrorum in situ*. The importance of nectar as fuel for heat production was clearly demonstrated on three occasions when the bees were found, first thing in the morning, almost motionless, without stores and the nest temperature only 1° C. above air temperature. Within 5 min. of filling the honey-pots with syrup the workers were fully active and the nest temperature had risen, in one case from 13 to 25° C., in another from 14 to 23° C., and in the third from 17 to 26° C.

(*e*) *Behaviour of foragers and house-bees in the nest*

Foragers were rarely in the nest for any length of time during the observation hours, but when present they were seen to perform nearly all the nursing duties usually carried out by the house-bees. These consisted primarily of incubation but included feeding the brood, building up the rims of honey pots, altering the wax covering the larvae and rearranging such nest material as was available. Even the queen, in addition to constructing all the wax egg cells, often fed the larvae and attended to their wax coverings although she too spent most of the time incubating.

No trend in duties was observed among the house-bees as they aged. Sometimes the same bee would be noticed on several days in succession fanning or tugging in nest material, but this was probably a matter of chance and habit rather than a further division of labour since subsequently these same jobs would be performed by another worker, the original one being occupied elsewhere.

(*f*) *The collection of pollen*

A further division of labour among the foraging workers was observed in the collection of pollen. The heavier bees tended to collect a larger proportion of pollen loads than the lighter; this is shown in Tables 6 and 7. The division appears to fall at about 150 mg. and the bees have been arranged arbitrarily into two groups, those above and those below that weight. When the total number of loads with and without pollen (considering only those days on which some pollen was collected by the colony as a whole) were compared for the two groups of bees by the χ^2 test a highly significant difference ($P < 0{\cdot}1\%$) was found in both years. This relative absence of pollen collecting by small bees could be brought about in two ways, either small bees may visit the same flowers as the large bees but fail to collect the available pollen or they may visit different flower species that produce little or no pollen. The former seems the more probable alternative for though it is quite likely that the smaller bees, having shorter tongues, may visit flowers with short corollas (when seeking nectar), as suggested by Cumber (1949), there is no evidence that less pollen is available from such flowers. When gathering pollen (see later) there was no relation between the size of the bee and the flowers visited, though inevitably data from the small bees was scanty.

Since the small house-bees do not normally take to foraging until the colony has passed its climax and the numbers of larvae are diminishing, the fact that they collect mainly nectar is probably an advantage, and led in 1947 to an apparent connexion between the amount of brood in the nest and the number of pollen loads brought in.

Table 6. *Number of pollen loads collected by workers in the* 1947 *nest*

Bee no.	Weight of bee (mg.)	Loads with pollen	Loads without pollen
10	220	32	10
22	190	23	7
9	180	49	4
20	170	30	33
13	160	28	7
12	160	26	11
15	160	23	10
6	150	37	5
21	150	12	2
	Total for bees of 150 mg. and over	260	89
17	140	12	29
8	140	31	10
18	140	0	32
25	120	0	13
19	110	1	22
1	90	1	11
	Total for bees less than 150 mg.	45	117

Table 7. *Number of pollen loads collected by workers in the* 1948 *nest*

Weight of bee (mg.)	Loads with pollen	Loads without pollen
230	15	4
190	14	14
160	9	3
Total for bees over 150 mg.	38	21
140	4	6
130	4	10
120	7	35
110	5	7
110	12	9
100	0	22
100	7	6
100	0	22
90	0	11
Total for bees less than 150 mg.	39	128

That there was no real response on the part of the bees to the requirements of the colony was shown, however, by the fact that one or two of the larger bees and the queen herself at the end of the season still brought in pollen when there were only pupae in the nest. This pollen was perforce deposited in a honey-pot, no pollen pockets being available; here it accumulated indicating that more was being brought in than the adults themselves required. In 1948 pollen collection bore no relation to the numbers of larvae in the nest.

(*g*) *Discussion*

The foraging bees in a nest can thus be divided roughly into two groups, large bees beginning to forage early in life and collecting pollen as well as nectar and small bees beginning to forage late in life and collecting nectar only. Table 8 lists all those bees which had a reasonably extensive foraging record and whose age-at-first-foraging was known. It is apparent that heavy weight, early foraging and pollen collection went together in most cases although there were a few exceptions. The different size of

Table 8. *Weight, age-at-first-foraging, and pollen collection of workers in* 1947 *and* 1948 *nests*

Bee no.		Weight (mg.)	Age at first foraging (days)	Pollen loads as % of total loads
1947	*10*	220	4	76
	22	190	6	77
	9	180	5	93
	20	170	4	48
	13	160	7	80
	12	160	7	70
	15	160	6	70
	21	150	3	86
	17	140	6	29
	18	140	15	0
	25	120	11	0
	19	110	14	4
1948	·	160	5	75
	·	140	4	40
	·	130	4	28
	·	120	5	17
	·	110	6	57
	·	100	8	54
	·	100	28	0
	·	100	15	0
	·	90	4	0

bumble-bee workers is usually considered to result from unequal larval feeding (Sladen 1912); if this is true the basis of the behaviour differences in the adults must be phenotypic. In the honey-bee Ribbands (1950) has found that anaesthetization with carbon dioxide or nitrogen eliminated pollen collection tendencies and caused the treated bees to begin foraging much earlier than the untreated ones. It would seem possible therefore that in the social bees pollen collection and age-at-first-foraging are rather more easily altered by external conditions than other types of behaviour such as nectar collection and care of the brood.

FORAGING

(*a*) *Behaviour of foragers when discharging loads in the nest*

Normally a forager would only spend 1 or 2 min. in the nest between journeys. In this time she would, if carrying pollen, choose a pollen pocket and deposit her loads therein, usually turning round to press the loads down herself. If carrying nectar, unless molested (see later), she discharged it direct into a honey-pot. Then after cleaning wings and antennae she would leave the nest again. Most bees collected

pollen and nectar together, for example from 7 to 31 July 1947 of the 219 pollen loads recorded 164 (75%) were accompanied by nectar. When carrying a double load either commodity was discharged first but a great many receptacles were often visited before the loads were actually deposited. There was apparently some reason for this fastidiousness often recorded by other observers (Sladen 1912). As regards pollen there were not usually more than two or three pollen pockets to choose from but although there were always several honey-pots available, without leaks and apparently suitable, the choice was not random. Thus on 26 July 1949, although there were about thirty honey-pots empty, the nine foragers used only three pots depositing six loads in one, six in another and two in a third. On 29 July the first pot of 26 July was not in use, but three loads were deposited in the second, four in the third and five in a new pot, the fourth. On 30 July the four loads observed were all placed in the second pot. On 4 August the first and second pots were in use and also a fifth one. It seems, therefore, that the bees will if possible deposit their nectar in a pot already partly filled and only start to use a new one when the originals are full.

Often after discharging a nectar load a worker left the nest with pollen still on her legs (one potential cause of mixed pollen loads). It cannot certainly be said that this did not occur with nectar loads as well, but this seems improbable since several times workers that were seen leaving the nest chamber proper without having discharged nectar, turned round in the vestibule and returned to the nest to do so. In addition, foragers known to have drunk freely from syrup supplied by the author within the nest never left without first emptying their honey-stomachs. On several occasions when the honey-pots in use at the time had been filled with sugar syrup in this way, the incoming foragers drank (the bees evidently did not load themselves to capacity in the field) and then remained in the nest for much longer than usual, building up the rims of the honey-pots or incubating brood until eventually they discharged their nectar and left the nest. In this way it was possible to keep the whole population in the nest in the middle of the day.

(*b*) *Duration of foraging journeys*

During the 2 years 665 foraging trips were timed, 381 in 1947 and 284 in 1948. The average time of absence from the nest was 17·5 min. in 1947 and 15·3 min. in 1948; by analysis of variance this difference, the reason for which will emerge later, was highly significant ($P < 0{\cdot}1\%$). The range of times was very large, from 2 to 52 min. There are a number of possible causes for the great variation in the duration of foraging trips and some of these, type of load, rainfall, temperature and individuality of the bees, were investigated. The first two were found to be important. In considering the type of load pollen loads, with or without nectar, have been contrasted with loads of nectar only. Pollen loads took longer to collect than loads of nectar; 18·6 and 16·3 min. for loads with and without pollen in 1947 and 24·2 and 19·3 min. for loads with and without pollen in 1948 ($P < 0{\cdot}1\%$, only those days on which some pollen was collected being considered). The effect of rain was more marked. Considering all days and all types of load in the 2 years, foraging trips averaged 13·6 and 13·2 min. on days when rain fell and 18·8 and 21·5 min. on days when no rain fell (for this difference $P < 0{\cdot}1\%$). The difference was most marked for

the nectar-only loads, presumably because a large amount of dilute nectar was available. It was noticeable that on damp days (the bees foraged unless rain was very heavy) the house-bees excreted very frequently and evidently had to drink more of the dilute nectar to maintain their activity. Incidentally the great difference in the amount of rainfall in the 2 years (August 1947: 0·04 in.; August 1948: 7·84 in.) accounts for the fact that the average time for all journeys was lower in 1948 than in 1947 although under similar conditions the 1948 bees were slightly longer on foraging trips than the 1947 bees.

Of the other two factors mentioned, temperature had no detectable effect on the duration of foraging trips and the times of individual workers could not be satisfactorily compared since they foraged over different periods with varying weather conditions.

(*c*) *Composition of pollen loads*

In 1947, 120 pollen loads were taken from the workers as they were brought into the nest. The pollens were identified and classed as either major or minor constituents of the load. It is well known that bumble-bees visit different plant species on any one foraging trip, and in this colony of *B. agrorum* rather more than half the loads were mixed. Out of 120 loads identified 53 were unmixed, 37 were mixtures of two, 19 mixtures of three, 9 mixtures of four and one each mixtures of five and six different plant species. Clements & Long (1923) examined 102 pollen loads taken from thirteen American species of *Bombus* in the field. Their corresponding figures were: 50 pure loads, 45 mixtures of two, 6 mixtures of three and 1 mixture of four different plant species. Comparing the two sets of data by the χ^2 test, *B. agrorum* had a significantly higher proportion ($P < 1\%$) of mixtures of more than two plant species than the American Bombidae.

Table 9 shows the collection of some of the individual bees. The mixing was not entirely fortuitous, *Vicia* with red and white clover tending to form one group and *Centaurea nigra*, *Lotus corniculatus* and *Rubus* another. This division conformed roughly with the distribution of these plants in the immediate neighbourhood of the nest. The first group of plants all grew together in a meadow, while *Lotus corniculatus* and *Centaurea nigra* occurred on a bit of waste land bounded by a hawthorn hedge (*Crataegus* sp.) with blackberry (*Rubus* sp.) intermingled.

Some bees seemed to be fairly constant to one group of plants, occasionally making a complete change (e.g. bee *10*; this break may have been the result of cutting the hay), others, especially bee *13* were more catholic in their choice. All the bees except one collected both pure and mixed loads. Bee *6* confined its attention for the 4 days that it was watched to red clover, and considering all the pollen loads together more pure loads were collected from this than from any other plant. Thus, of the loads listed in Table 9, red clover occurs with other pollens in twenty-six loads and alone in twenty-two; for *Lotus corniculatus* the corresponding figures are 33 : 2, for *Centaurea nigra* 35 : 6 and for *Vicia* 19 : 2. When two or more loads were taken from a bee on one day they were not always the same but the figures are too small to determine if any regular daily changes (due to different times of pollen availability (Synge 1947)) were occurring.

The direction in which the bees flew when leaving the nest was noted in 1947. This

Table 9. *The pollen loads of individual workers in the* 1947 *nest*

Bee no.	... 6	8	9	10	13	12	15	21	17	20
7 July	R R	·	·	·	·	·	·	·	·	·
8	R R	P	·	·	·	·	·	·	·	·
9	·	P R	·	·	·	·	·	·	·	
10	R	Vr R R	V	·	·	·	·	·	·	·
11	·	·	RV	·	·	·	·	·	·	·
12	R	R	V RV	·	·	·	·	·	·	·
13	·	R	·	·	·	·	·	·	·	·
15	·	·	·	RW	·	·	·	·	·	·
17	·	Pr R R	RV RVW	RVp	·	·	·	·	·	·
18	·	·	VR VR	R R R	·	·	·	·	·	·
24	·	·	Rvp Rvp	B B B	Pw Mb	K Kv K VK	VK	·	·	·
25	·	·	Rvpk Rvp	B Bl BL	P RV	Lkr K K Kvl	P L	·	·	·
26	·	·	·	Lbk Lrk	Kl	Kl	·	Wr	Lkv Kl	·
27	·	·	·	BLKs BLK B	·	Lkag	L	Lrwk	·	·
29	·	·	K	·	RLw	RLvpkx	·	·	·	
30	·	·	·	Lbks	·	RKwp	P P Lkv	LW	·	TC T
31	·	·	·	Lb	B	RWk	·	·	·	T T
1 Aug.	·	·	·	·	Ks HZ	·	·	·	·	·
2	·	·	·	·	Z	·	·	·	·	·
3	·	·	Z	Lkbq	LK	·	·	Lkq	·	·
4	·	·	W	Lb	·	·	·	RW	Lkr	T
5	·	·	·	·	·	·	·	·	Lk	Tk
6	·	·	·	Lbk	K	·	·	RW	RWKla	·
8	·	·	Wk	·	·	·	·	·	Lk	·
10	·	·	Lwk	·	·	·	·	·	Lk	Tmc
13	·	·	·	·	·	·	Lk	·	·	·
18	·	·	·	·	·	·	Lk	·	·	·
19	·	·	·	·	·	·	R	·	·	·
20	·	·	·	·	·	·	R R	·	·	·
22	·	·	·	·	·	·	R R	·	·	·
31	·	·	·	·	·	·	R	·	·	·

Capitals = major constituent of load; small letters = minor constituent of load.

A = *Aster* type
B = *Rubus*
C = Cynareae
G = Gramineae
H = *Crepis* type
K = *Centaurea nigra* L.
L = *Lotus corniculatus* L.
M = *Melandrium rubrum* (L.) Coss. & Germ.
P = *Prunella vulgaris* L.
Q = *Tilia*
R = red clover
S = *Succisa pratensis* Moench
T = *Teucrium scorodonia* L.
V = *Vicia*
W = white clover
X = *Plantago*
Z = *Ranunculus*

nest was kept in a caravan situated on the north side of a tall hedge running south-east to north-west, and the nest was at the south-eastern end of the caravan. Five different routes could be distinguished and were numbered 1 to 5. Bees leaving by route 1 turned to the right immediately on leaving and then flew between the caravan and the hedge in a north-westerly direction. Bees leaving by route 5 turned immediately to the left and after passing the caravan also flew in a north-westerly direction. Route 2 led through a gap in the hedge to the field on the south side, while route 3 went straight along the hedge to the south-east. Route 4 was rather less well defined by landmarks but bees flying in this direction rose sharply up a rocky slope to the east. In Table 10 the records for nine of the bees are given. The numbers are arranged

Table 10. *The direction in which bees left the* 1947 *nest*

Bee no.	Routes taken arranged chronologically
9	4 1 1 4 4 1 1 1 1 1 4 1 1 1 1 1 1
10	1 1 1 5 1 1 1 1 1 1 1 1 1 1 5 1 1 1 1 1 1 1 1 1 1
12	1 1 5 5 5 1 1 1 1 5 1 1 1 5 1 5 5
13	2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 4
15	2 4 4 4 4 4 4 4 4 4 4 4
17	4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4
20	5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3
21	5 5 5 5 5 5 5 5 5 5 5 5 5
22	2 5 5 5 5 5 5 5 5 5 5 5

Table 11. *Pollen collection of the* 1947 *colony as a whole*

(Figures give the number of loads in which each type of pollen formed a major or minor constituent.)

	Major	Minor	Total loads
Red clover	61	8	69
Lotus corniculatus	32	3	35
Centaurea nigra	19	25	44
Vicia	13	8	21
Rubus	13	6	19
White clover	10	5	15
Prunella vulgaris	8	7	15
Teucrium scorodonia	7	0	7
Ranunculus	3	0	3
Melandrium rubrum	1	1	2
Crepis type	1	0	1
Cynareae	1	1	2
Aster type	0	2	2
Succisa pratensis	0	3	3
Tilia	0	2	2
Viola	0	1	1
Gramineae	0	1	1
Plantago	0	1	1

chronologically but cover several observation hours and do not necessarily refer to successive journeys. The results from this line of evidence agree with those from the pollen loads; each bee has moderately fixed foraging habits, fairly frequently deviated from and occasionally completely abandoned for others. It is known from observation of marked bees that for a number of days bumble-bees, like honey-bees, will visit the same area repeatedly and such uniformity in pollen collection and direction of flight as exists is probably attributable to this. Bee *20*, who collected almost entirely from *Teucrium scorodonia*, must certainly have confined its activities to a small area for only one patch of the plant grew in the neighbourhood.

The pollen collection of the colony as a whole will not be considered in detail here as the matter has been investigated for other nests by analysis of larval meconia and the results given elsewhere (Brian 1951*a*). By both methods of sampling red and white clover, *Lotus corniculatus* and *Vicia* were found to be the main pollen plants of *Bombus agrorum* in this neighbourhood, but the observation nest in addition had collected appreciable amounts of *Centaurea nigra* and *Rubus* pollens (Table 11), the latter mainly due to one bee, no. *10*.

BEHAVIOUR OF THE BEES TOWARDS ONE ANOTHER

(*a*) *Normal behaviour*

Bombus agrorum workers behave very independently in the nest. Normally there is no exchange of nectar, as in most other social hymenoptera, nor has anything in the nature of the information-giving dances described by von Frisch (1950) for the honey-bee ever been observed. Consequently, a house-bee shows little interest in the coming and going of foragers nor in the movements of other house-bees. While in the nest each worker divides its time between periods of rest, when it remains quietly incubating the brood, and periods of activity which may be described as 'patrolling' during which it will perform any job, larval feeding, nest repairing, etc., which it finds requires attention. There is no synchronization of patrolling and resting among the workers present in the nest.

Only a few situations call forth concerted action, chiefly disturbance of the nest and breaking open of the cells. Sudden filling of the honey-pots causes all the workers to help in building up the rims and the discovery by one or two workers of an easily obtained source of nest material may, when it is scarce, lead to all workers helping in its collection.

(*b*) *Exceptional behaviour*

A very few exceptions to this rule of mutual tolerance or indifference, when one worker has attacked another, have been observed. These attacks have only been seen on twenty-one occasions in 3 years but are given significance by the fact that only a few particular individuals were involved and the attacks were not indiscriminate.

In the 1947 nest, worker no. *1*, already mentioned for its exceptional longevity and the fact that it took to house duties after a spell of foraging (a near queen type), was always the aggressor. She attacked bee *4*, a house-bee on 25 July, 2 days before this bee disappeared. The other three attacks were all made upon bee *15* on 31 July, and 2 and 5 August. Bee *15*, as already mentioned, was exceptional in that it began to forage early but then abandoned foraging for several days; it was during this period, before it resumed foraging, that it was attacked by bee *1*.

In 1948 only two worker attacks were seen, both on 9 September when one house-bee twice attacked a certain forager. Neither bee was outstanding in any way. It was in this nest that the queen repeatedly (fourteen times from 14 to 30 August) attacked one particular house-bee (Brian 1951*b*). This bee was exceptional in three ways; she was a forager who later turned to house duties, she attained a considerable age and she was the only laying worker recognized in any of the three nests (another near queen type). She always attempted to lay eggs in the cells made by the queen and on the same days that the queen herself laid. The queen's attacks however were

not confined to driving the worker from the egg cells but took place whenever the two bees met upon the comb, indeed the worker apparently attempted to avoid the queen on many occasions.

In 1949, fifteen attacks were observed and in twelve of these the aggressor was one particular house-bee, unfortunately of unknown age. The other three were single attacks by three different house-bees. The attacked were always foragers except in one case when the bee changed from house duties to foraging the day following the attack. Sometimes the forager was attacked after discharging her load and on two occasions this caused her to leave the nest immediately without the usual cleaning preliminaries. On four occasions, when the forager had been attacked as soon as she entered the nest, she was forced to half-extend her tongue and discharge a drop of nectar which was drunk by the attacker or fell to the floor, though on one occasion the attacked managed to reach a honey-pot with the drop still hanging from her mouth. These were the only times at which liquid was seen to pass from bee to bee in any of the nests; every other time the foragers discharged their load direct into a honey-pot from which other workers and the queen would feed themselves. The attacks were not motivated by hunger as there was nectar present in the nest each time.

To summarize, although in the 3 years ninety-eight workers were marked and watched only six were seen attacking and thirteen being attacked. In every case the attackers were house-bees and the attacked were either foragers or, in a few cases, bees that took to foraging following the attack.

(*c*) *Discussion*

These observations on the inimical behaviour of *B. agrorum* workers, although few, are strongly reminiscent of the dominance behaviour of *Polistes* wasps, described by Pardi (1948), who indeed predicted that 'phenomena of competition' would be found to occur among the Bombini. He describes five behaviour patterns used in contacts between dominant and dominated workers in which the dominant worker behaves in a progressively more ferocious manner. Of these the fifth and final pattern, where the dominant worker bites violently, clasps the dominated worker with the legs and sometimes stings or attempts to sting while the dominated worker offers a drop of liquid, runs away quickly taking shelter behind the comb or in the cells or goes out of the nest, seems best to describe the position in *Bombus agrorum*, though less violent contacts, chiefly avoidance of the attacker, may also occur.

When so few attacks have been observed it cannot be said that *B. agrorum* shows a dominance order comparable to that of *Polistes*, but there are many points of resemblance. In dominant *Polistes* workers four characteristics are associated: (*a*) attacking of other workers, (*b*) absence of foraging, (*c*) relatively old age, and (*d*) development of the ovaries. The *Bombus agrorum* data is scanty and all four characteristics were never found in any one bee, but various combinations of these characteristics occurred. Thus in the 1947 nest (*a*), (*b*) and (*c*) were associated in one worker (no. *1*) and in a worker of the 1948 nest (*b*), (*c*) and (*d*) were associated. In 1949, (*a*) and (*b*) were associated in four workers whose age unfortunately was not known. Unless a worker had begun to lay eggs it was impossible to find out, in this study, whether its ovaries were developed, since the bees obviously could not be killed and very rarely died in

the nest. However, Sladen (1912, pp. 53 and 241) records that in several species of *Bombus* egg-laying by workers following the death or decline of the queen was always accompanied by quarrelling, which provides evidence that (*a*) and (*d*) are frequently associated. From this it seems probable that the factors making for dominance in *Polistes* and *Bombus agrorum* may well be the same.

The results of dominance would also seem to be the same in the two species. The dominant *Polistes* worker rests on the front of the comb, the subdominant behind; in *Bombus agrorum*, workers liable to be attacked tend to hide in the lower regions of the nest among the old cocoons. In both species the dominant worker remains in the nest while the dominated forages. The dominant worker has a trophic advantage, obtaining more liquid from the foragers, directly in *Polistes*, indirectly (via the honey-pots) in *Bombus agrorum*. There would thus appear to be a reasonable parallel in behaviour between *Polistes* and *Bombus agrorum*, but whereas the dominance order is an essential feature of colonial life in *Polistes* wasps it is only rudimentary or vestigial in *Bombus agrorum*.

SUMMARY

1. The behaviour of workers marked individually has been studied in four observation nests of *B. agrorum*.

2. Both large and small workers foraged and undertook house duties; the apparent division of labour previously noted results from the later age at which small workers begin to forage, about 15 days from emergence as against 5 days for the large workers.

3. By manipulation of colonies it was found that neither absence of foraging bees nor absence of nectar caused the small house-bees to begin foraging. It was therefore considered to be a matter of ontogeny.

4. The longevity of the workers was variable, 69 days being the maximum recorded. On the average 29% of the bees died every 5 days. House-bees lived slightly longer than foragers, particularly in a bad season.

5. About two-thirds of the total bee population were house-bees and one-third foragers at any particular time.

6. No trend in duties with age was observed in the house-bees, foragers, when in the nest, performing a variety of house duties.

7. The larger foragers collected pollen and nectar, 75% of pollen loads being accompanied by nectar. The smaller foragers tended to collect nectar only.

8. In all, 665 foraging trips were timed, the averages for two nests being 17·5 and 15·3 min. Pollen loads with or without nectar took longer to collect than nectar loads alone and loads were collected faster in damp weather than in dry.

9. Pollen loads from one nest were collected and identified. Out of 120 loads, sixty-seven were mixtures of from two to six plant species. The pollen collection of individual workers indicated moderately fixed foraging habits.

10. Normally the workers behaved indifferently towards each other but on a very few occasions attacks were observed in which the attacked bee was forced to disgorge liquid or leave the nest. The attacker was always a house-bee, the attacked a forager. A comparison with the dominance order in *Polistes* wasps is made.

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THE RELATION OF THE RADULA FRACTION TO THE ENVIRONMENT IN *PATELLA*

By M. V. BRIAN and G. OWEN*
Department of Zoology, University of Glasgow

(With 1 Figure in the Text)

During the summer of 1949 the distribution of the species of *Patella* around the Pembrokeshire coasts was investigated. As an aid to the identification of the species the radula fraction, radula-length divided by shell-length, was determined (Fischer-Piette 1935). It was noticed that in the case of *P. vulgata* L., the results suggested that there might be a correlation between the value of the radula fraction and the position of the animal relative to high and low water. This has now been fully investigated.

Samples of *P. vulgata* were obtained from five localities on the west coast, namely: Dale Fort, Pembrokeshire; Llantwit Major near Cardiff; Clachan Bridge, Easdale and Luing Island in Argyllshire. In each case specimens were collected from high- and low-water habitats, i.e. about and above high-water neaps and about and below low-water neaps. The length of the shell was measured with a vernier gauge. The buccal mass was opened and the radula carefully withdrawn and measured. Care was taken that no specimens of *P. depressa* Pennant and *P. aspera* Lamark were included in the samples.

Considerable confusion exists over the nomenclature of the British species of *Patella*. In the *Plymouth Marine Fauna* (1931) the species are *P. vulgata* L., *P. depressa* Pennant and *P. athletica* Bean. Fischer-Piette (1935) described the three species as *P. vulgata* L., *P. intermedia* Jeffreys and *P. depressa* Pennant respectively. Thus *P. depressa* Pennant has been used to denote two different species. Eslick (1940) and Orton (1946) followed the nomenclature used by Fischer-Piette (1935), while Winkworth (1932) and Evans (1947) followed the nomenclature given in the *Plymouth Marine Fauna*. Fischer-Piette (1938) has established that *P. athletica* Bean 1844 is the species named *P. aspera* by Lamark in 1819, while Tomlin (1923) has established that *P. depressa* Pennant 1777 is *P. intermedia* Jeffreys 1865. Fischer-Piette (1948) has recently stated that the name *depressa* was applied to *P. aspera* (*P. athletica* Bean) in error. To avoid confusion Fischer-Piette (1938 and 1948) has continued to use the name *intermedia*. In this paper, following the rules of international nomenclature, it is proposed to use *P. vulgata* L., *P. depressa* Pennant and *P. aspera* Lamark; for convenience the names are tabulated below with those adopted by recent workers.

P. vulgata L.	—
P. depressa Pennant 1777	*P. intermedia* Jeffreys 1865 as used by Fischer-Piette (1935, 1938 and 1948), Eslick (1940) and Orton (1946)
P. aspe a Lamark 1819	*P. athletica* Bean used in the *Plymouth Marine Fauna* (1931) and by Winkworth (1932) and Evans (1947)
—	*P. depressa* used by Fischer-Piette (1935), Eslick (1940) and Orton (1946)

* G. Owen collected, identified and measured the samples, while M. V. Brian was responsible for the statistical analysis of the results.

ANALYSIS OF MEASUREMENTS

The results have been analysed by the method of covariance and, in addition, discriminant functions have been calculated for each locality (Mather 1949).

In all five samples (Table 1) the average shell-length of low-water *P. vulgata* exceeds that of high-water *P. vulgata* and, conversely, the average radula-length of high-water *P. vulgata* exceeds that of low-water *P. vulgata*. There is, however, no consistently statistically significant difference between top- and bottom-living animals that can be based on either of these variates alone. In three cases average shell-length differs significantly at the two levels, and in three cases average radula-length also differs significantly; but in only one station do they both differ significantly.

Table 1. *Summary of the shell and radula measurements of* Patella vulgata

		No. of observations	Average shell-length	Average radula-length	Ratio of averages	Regression coefficients	Adjusted shell-length means
Luing Island	High	58	32·95	64·29	1·95	0·4403	31·27
	Low	52	34·99	55·80**	1·59	0·3828	36·86**
Easdale	High	39	36·02	70·58	1·96	0·3262	34·03
	Low	38	37·59	58·33**	1·55	0·3350	39·63**
Llantwit Major	High	49	29·12	56·86	1·95	0·3496	28·07
	Low	51	32·12*	51·73	1·61	0·4457**	33·12**
Dale Fort	High	12	38·68	70·63	1·83	0·3677	36·44
	Low	17	45·27*	62·68	1·38	0·7405*	46·85*
Clachan Bridge	High	33	36·23	66·56	1·84	0·2483	34·50
	Low	30	39·32*	56·31**	1·43	0·4627**	41·22**

* Difference significant: P between 0·01 and 0·05.
** Difference highly significant: $P < 0{\cdot}01$.

Consistent properties appear only when the two variates are considered together. In all five stations the means regress negatively while the data within levels regress positively, and linearly ($P < 0{\cdot}01$). Graphically, these properties mean that the line relating the two variates in the lower habitat lies above that in the higher habitat (Fig. 1). Thus, since the differences in average radula-length at the two levels are substantial, even if not significant, the regression within levels has a material effect on the mean shell-lengths causing them (on account of the negative regression between averages) to lie nearer together than would otherwise be the case. Adjustment of the data to a constant radula-length thus leads to an increase in the difference between average shell-lengths at the two levels. These adjusted differences are, moreover, in all five cases statistically significant ($P < 0{\cdot}01$ in four cases, and 0·05–0·01 in specimens from Dale Fort). Hence, the graphical position of the lines, one above the other, may be taken to portray a real biological difference between the populations. Using these results it would be possible, from a mixture of high- and low-water *P. vulgata*, to identify one or other type in over 78% of cases; if a discriminant function were used this could be increased to over 80%. For comparison it may be noted that using one or other of the variates alone (whichever is more useful), no more than 65–70% of a mixed sample could be correctly allocated.

(*a*) *Luing Island*

In this locality high- and low-water samples of *P. vulgata* were collected from a fairly smooth rock surface inclined at an angle of 40 degrees to the sea. The region was very exposed to wave action and the dominant fauna consisted of barnacles and limpets. Specimens of *P. aspera* were common. The regression equations for the two levels are:

$$\hat{Y} = 0{\cdot}4403X + 4{\cdot}64 \text{ (top)},$$
$$\hat{Y} = 0{\cdot}3828X + 13{\cdot}63 \text{ (bottom)}.$$

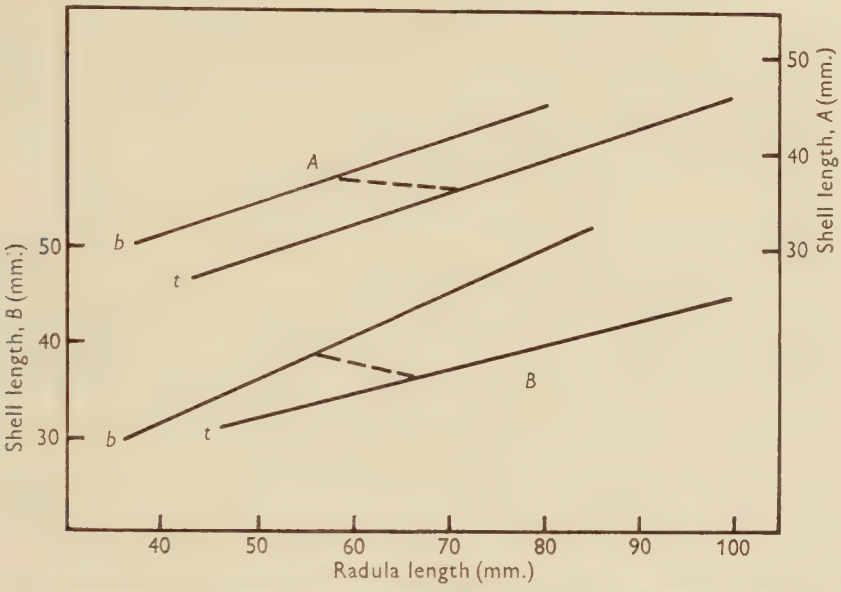

Fig. 1. The regression of shell-length on radula-length at two water-levels in two localities. *A*, Easdale; *B*, Clachan; *t*, higher level; *b*, lower level. Each line covers the full range of radula-length observed but is not extrapolated. The means are connected by broken lines.

Here and throughout the paper $\hat{Y}$ = the expected shell-length in mm. and X = the radula-length in mm. The regression coefficients do not differ significantly ($P > 0{\cdot}1$). Adjustment of the shell-means using the average within-level regression coefficient ($b = 0{\cdot}4173$) increases the difference between them from 2·04 to 5·50 (see Table 1). Thus, for a given radula-length, shells from lower levels are longer than those from higher levels on the shore. The discriminant function (F) has the form;

$$F = 0{\cdot}004468\,Y - 0{\cdot}002293X.$$

Classification based on Y alone gives 56% success, on X alone 62% success, on both X and Y 79% success and using the discriminant function, 81% success.

(*b*) *Easdale*

Here, as at Luing, the locality chosen was very exposed to wave action and specimens of *P. aspera* were common. The regression equations (see also Fig. 1) are:

$$\hat{Y} = 0{\cdot}3262X + 13{\cdot}00 \text{ (top)},$$
$$\hat{Y} = 0{\cdot}3350X + 18{\cdot}05 \text{ (bottom)}.$$

Again the coefficients do not differ significantly ($P > 0{\cdot}1$), but the average regression coefficient ($\bar{b} = 0{\cdot}3296$) is less than that of the data collected from Luing ($P = 0{\cdot}05$). Adjustment increases the difference between shell-means from 1·57 (the smallest of the five differences) to 5·60. Thus, in this case too, the shell-length of the low-water *P. vulgata* is larger for a given radula-length than that of the high-water *P. vulgata*. The discriminant function has the form $F = 0{\cdot}005802Y - 0{\cdot}003200X$. Classification based on Y alone gives 56% of successes, on X alone 71%, on both X and Y 78% and using the discriminant function, 84%.

(*c*) *Llantwit Major*

The beach at Llantwit falls gradually in a series of steps towards L.W.M. and the area is moderately exposed to wave action. *P. vulgata* is the only one of the three species present. The regression equations are:

$$\hat{Y} = 0{\cdot}3496X + 9{\cdot}24 \text{ (top)},$$
$$\hat{Y} = 0{\cdot}4457X + 9{\cdot}06 \text{ (bottom)}.$$

Here the coefficients differ significantly ($P < 0{\cdot}01$), but the lines diverge from a point ($Y = 9$, $X = 0$) well outside the population data. Thus, through the relevant part, the high-level line lies below the low-level line. Using the average regression coefficient within levels the difference between average shell-lengths at the two levels may be increased from 3·00 to 5·05 units. The discriminant function has the form

$$F = 0{\cdot}007082Y - 0{\cdot}003073X.$$

Classification based on X alone gives 57% success, on Y alone 59%, on X and Y 82%, and using the discriminant function, 83% success.

(*d*) *Dale Fort*

This beach lies completely inside Milford Haven and is fairly sheltered from wave action. Occasional specimens of *P. aspera* are present near L.W.M. but *P. depressa* is rare, only two specimens being found near M.T.L. after a thorough investigation of the beach. The regression equations are:

$$\hat{Y} = 0{\cdot}3677X + 12{\cdot}71 \text{ (top)},$$
$$\hat{Y} = 0{\cdot}7405X + 1{\cdot}14 \text{ (bottom)}.$$

The difference between the coefficients is in this case also significant (P, 0·05–0·01). The lines diverge from a point ($Y = 25$, $X = 35$) at the lower level of the population range—the smallest shell had the dimensions $Y = 24{\cdot}1$, $X = 40{\cdot}0$. Thus, as elsewhere, the line for high-level *P. vulgata* lies below the line for low-level *P. vulgata* throughout their relevant parts. Adjustment, using the average regression coefficient within levels ($\bar{b} = 0{\cdot}4817$), increases the difference between average shell-lengths from 6·59 to 10·41. The discriminant function is as follows: $F = 0{\cdot}0139Y - 0{\cdot}008304X$. Success in distinguishing high- and low-water *P. vulgata* increases from estimates based on X alone (61%), on Y alone (65%), on X and Y (80%), to 84% when the discriminant function is used.

(e) *Clachan Bridge*

This sample was collected from the mainland shore bordering the narrow stretch of water between Seil Island and the mainland. The area is entirely protected from wave action and *P. vulgata* appears to be the only species present. The regression equations (see also Fig. 1) are:

$$\hat{Y} = 0{\cdot}2483X + 19{\cdot}70 \text{ (top)},$$
$$\hat{Y} = 0{\cdot}4627X + 13{\cdot}27 \text{ (bottom)}.$$

Again the difference between the regression coefficients is highly significant ($P < 0{\cdot}01$) and they form two lines diverging from a point ($Y = 27$, $X = 30$), as in the previous case, near the smallest observation ($Y = 26{\cdot}1$, $X = 36{\cdot}3$). Thus, the line for high-water *P. vulgata* lies below the line for bottom *P. vulgata* throughout the relevant portions. Using the average regression within levels ($b = 0{\cdot}3543$) to adjust the shell-length means, the difference is increased from 3·09 to 6·72. The discriminant function is as follows: $F = 0{\cdot}006921\,Y - 0{\cdot}003490X$. Classification based on Y alone gives 60% success, on X alone 66%, on X and Y 80%, and using the discriminant function, 82% success.

It will have been noticed that in three of the stations (Llantwit, Dale Fort and Clachan) the within-level regression lines diverge (as in Fig. 1*B*) and in two they are parallel (as in Fig. 1*A*). In these two the average slopes, $b = 0{\cdot}4173$ (Luing) and $b = 0{\cdot}3296$ (Easdale), differ significantly (P, 5%).

There is evidence that the extremes of form between the two levels are connected by a gradual transition. Animals were collected from six different heights above chart datum on the Pembrokeshire coasts and measured as before. The value of the mean radula fraction for these specimens is given in Table 2. A gradual trend of increase with height above chart datum is apparent.

Table 2. *Height above chart datum and the mean radula fraction in* Patella vulgata

Height above chart datum (ft.)	Mean radula fraction	No. of specimens
2– 5	1·60	32
5– 8	1·64	36
8–11	1·70	23
11–13	1·72	63
13–15	1·78	59
15–17	1·96	100

INTERPRETATION OF RESULTS

Both Eshick (1940) and Evans (1947) attempted to relate the value of the radula fraction in *P. vulgata* to the age and size of the individual but without success. The conclusion that the value of the radula fraction differs in high- and low-water *P. vulgata* is, however, inescapable. *P. vulgata* from the higher levels tend to have a higher radula fraction than those from the lower levels. This correlation of radula fraction and vertical level could result from the effect of environmental factors on either the shell or radula, or on both simultaneously. The difference between high- and low-water animals could of course be genotypic, but a phenotypic explanation is

available as the subsequent argument shows; and in any case the latter makes a simpler working hypothesis. Success in identifying one or other type from a mixture of high- and low-water *P. vulgata* is considerably increased when the radula fraction is used, as compared with the use of either the shell-length or radula-length alone. Thus it is reasonable to conclude that the correlation of the value of the radula fraction and the vertical level results from the effect of environmental factors on both the shell and the radula.

The cause of variation in shell-shape in *P. vulgata* has been the subject of much discussion. Russell (1907), comparing high- and low-water limpets, found that high-water limpets were at all stages higher spired than low-water limpets. Russell concluded that this difference was due to those factors in which a high-water environment differed from a low-water environment. Orton (1933) correlated these differences of shell-shape with degrees of exposure to drying. He suggested that animals exposed to the risk of desiccation would contract down on to the substrate and produce relatively taller and narrower-based shells than those animals with a more expanded mantle living in damper conditions. Moore (1934) was able to produce striking proof of this by transferring marked animals from dry situations to rock pools. The effect on subsequent growth was shown by a pronounced ledge all round the shell. It is possible that these earlier workers included specimens of *P. depressa* and *P. aspera* in their samples. Orton (1946) has subsequently pointed out, however, that owing to the distribution of the three species the samples of *P. vulgata* examined by him (1933) for shell-shape must all have been *P. vulgata*, except possibly for occasional specimens of *P. depressa* among the low-water samples.

Thus, specimens of *P. vulgata* living in damp, sheltered situations do not contract the shell muscles to the same extent as those which have to resist desiccation and there is, therefore, less constraint on the lateral extension of the shell. Low-water *P. vulgata* would be exposed for a short period only and would tend to remain damp during the time they were left by the tide. In such animals the shell-length would be relatively longer than in high-water *P. vulgata* where the degree of exposure to desiccation would be considerably increased.

A consideration of the feeding habits of *P. vulgata* suggests a possible effect of environmental factors, associated with vertical level on the shore, on the radula-length. There has been considerable discussion as to the time the limpet leaves its home in search of food. Various workers have claimed that it wanders when covered by the tide, others that it wanders when uncovered. Russell (1907) found that limpets above 20 mm. or so in length did not wander when uncovered by the tide. In general, it would appear that limpets move about when the tide is in but that they also do so to some extent when uncovered, provided the rock is damp and the sun not too hot. Orton (1929) considered that the factors controlling the feeding movements of the limpet when uncovered appeared to be mainly those concerned with desiccation, and that there could be no doubt that the main feeding excursions were made in all habitats when the animals were covered by water. Jones (1948) states that at Port St Mary *P. vulgata* do not normally move when exposed to the air and that on bare rock they are usually on their homes when they are uncovered. As a result of these feeding habits low-water *P. vulgata* are able to spend a relatively longer time

feeding than high-water *P. vulgata*. The effect of this on the radula can only be surmised but it is reasonable to suppose that the result is a relatively shorter radula in low-water *P. vulgata* due to increased use.

There are good reasons for supposing that the differences observed in the value of the radula fraction are phenotypic. It is considered that the main factor governing the value of the radula fraction is the degree of desiccation to which the animal is exposed; it is probable that besides individual variation other factors, such as density of population and exposure to wave action, also affect the radula fraction. The effect of desiccation is to cause simultaneously an increase in one variate and a decrease in the other. The obscurity of a distinction attempted with a single variate would then result from the conflict between this inverse (negative) relationship with the direct (positive) relationship within-levels. This latter presumably represents in general a growth relationship but the actual form assumed by the animal, and so the slope of the regression line, would no doubt be affected by environmental factors as well. Hence, in the three stations with diverging lines, the environmental influence may have acted cumulatively, gradually differentiating an initially homogeneous and younger population. Why this effect was not detectable in the two other stations is not clear. The three 'divergent' stations were the ones in which a significant difference in mean shell-length was present, suggesting perhaps that the environment at the two levels differed more; but the radula differences were, in two of the three, so small as to be insignificant. Further consideration of these details is unprofitable for, as already suggested, many complexities of the actual habitat may be involved.

The correlation of the value of the radula fraction with environmental factors would appear to apply not only to the individuals within the species *P. vulgata* but also to the species within the genus *Patella*. Koch (1949) reviewed the South African representatives of the genus *Patella* and drew attention to the fact that the species inhabiting the more desiccated zones had the highest radula fractions. Among the British species of the genus, as Graham (1951) has recently stated, the 'wet form' of common limpet, *P. aspera*, has a radula which is, on the average, almost equal to the length of the shell, while the 'dry form', *P. vulgata*, has a radula which is almost twice the length of the shell. The case of *P. depressa* is more complicated. This species has a radula which is, on the average, more than twice the length of the shell. Orton (1946) considered both *P. depressa* and *P. aspera* to be low-water species, while Evans (1947) found that *P. depressa* was generally infrequent below M.L.W.N. This latter distribution is also true for the species round the Pembrokeshire coasts. *P. depressa* is also more or less restricted to surf-beaten, barnacle-covered rocks. Thus, it is difficult to regard exposure to desiccation as the main factor correlated with the high radula fraction in *P. depressa*. It is possible that exposure to wave action, which would have a similar effect on the radula fraction as exposure to desiccation, and a habitat of barnacle-covered rocks, which in *P. vulgata* affects shell-growth and radius of feeding (Jones 1948), are the main environmental factors affecting the radula fraction in *P. depressa*.

The extreme values given by Fischer-Piette (1935) and Evans (1947) for the radula fractions of *P. aspera* and *P. depressa* are shown in Table 3. The values found by Owen are for specimens collected from the Dale Peninsula, Pembrokeshire. Fischer-

Piette, on the basis of his figures, used the radula fraction to separate the two species. Evans (1947), however, claimed that the radula fraction alone was not to be trusted for the purposes of identification since the specimens collected by him from the Cardigan Bay area showed a considerable overlap (Table 3). The specimens collected from the Pembrokeshire area show a similar tendency. It should be pointed out, however, that the two specimens of *P. depressa* with the lowest radula fractions of those collected in this area (1·4 and 1·5) were obtained from a fairly sheltered beach and were, in fact, the only specimens of this species found away from wave-exposed conditions. From this present work it would appear likely that environmental factors have a considerable effect on the value of the radula fraction in all three species of *Patella*. This would suggest that at least some of the specimens of *P. depressa* collected by Evans were obtained from rather more sheltered conditions than were any of the specimens collected by Fischer-Piette (1935). To reduce the degree of overlapping Fischer-Piette (1948) related the radula length to the cube root of the volume of the shell.

Table 3. *Extremes for the value of the radula fraction in* Patella aspera *and* P. depressa

	P. aspera	*P. depressa*
Fischer-Piette (1935)	0·9 –1·4	1·6–2·5
Evans (1947)	0·78–1·6	1·2–2·4
Owen	0·7 –1·5	1·4–2·6

Fischer-Piette (1948) also compared the radula fraction of a conical form of *P. vulgata* from the upper zone of the beach with 'Les Patelles aplaties de Port Saint Hubert'. The mean radula fraction of fifty specimens of the conical form was 2·34 while that of fifty specimens from Port St Hubert was 1·50. Fischer-Piette considered these two forms of *P. vulgata* to be special ecotypes and not comparable with a 'normal' population of *P. vulgata*. This present work indicates that the value of the radula fraction may vary considerably within the same population and any investigation of the species of *Patella*, when considering the value of the radula fraction, should pay attention to the details of the environment and, in particular, to the degree of desiccation.

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SUMMARY

Patella vulgata L. were collected from high- and low-water levels on five different beaches and the lengths of the shell and radula measured. In all five localities the mean shell-length was less and the mean radula-length greater at the higher level, but the difference was not consistently statistically significant.

This complexity arose from the mergence of two conflicting tendencies: one, intralevel, a positive regression of shell-length and radula-length; the other, interlevel, a negative regression. Whilst the former is no doubt a growth phenomenon, the latter is probably an environmental effect—at the higher level exposure to desiccation and

consequently, prolonged adherence to the substrate, causes a smaller shell base: reduced feeding time causes a longer radula. These factors may have resulted in confusion when comparing the values of the radula fractions of species of *Patella*.

The intralevel regressions showed some variations: in three stations (all comparatively sheltered from wave action) they diverged from a point at the minimum population size and in two (exposed to wave action) they were parallel. The average slopes of the latter pair differed.

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THE PLACE OF AFRICA IN THE PALAEARCTIC MIGRATION SYSTEM

By R. E. MOREAU

Edward Grey Institute, Department of Zoological Field Studies, University of Oxford

(With 1 Figure in the Text)

INTRODUCTION

The migration of Palaearctic birds southward in autumn and northward in spring has long been recognized as one of the most remarkable biological phenomena. In modern times much attention has been given to the behaviour of the individual species and of the individual bird on migration and also some attention, though relatively very little, to the behaviour and ecology of the migrants in their winter quarters. But there has been no review of the Palaearctic migration as a whole in its essential aspect as a seasonal ecological adjustment on a gigantic scale.

In the present paper an attempt will be made to summarize the broad geographical facts which determine the main outlines of the migration system and which render Africa south of the Sahara (the Ethiopian Region) of paramount importance in the survival of many species prominent in the Palaearctic avifauna. The climates which the migrants encounter during their stay in the Ethiopian Region and the habitats into which they distribute themselves will then be briefly described and the problem of competition in their winter-quarters will be discussed. Finally it will be emphasized that, owing to changes in both the Palaearctic and Ethiopian environments, the details of the migration system are always changing; and some extreme differences that can be deduced to have occurred in the past are indicated.

For the present purpose information about the distribution of Palaearctic birds in their breeding ranges and in their winter quarters outside the Ethiopian Region is derived from Hartert (1910–38). Data relating to Africa are taken from the compilations of Sclater (1924–30) and Grote (1930, 1931, 1937), supplemented by later, incidental, references and by unpublished observations by myself and others, which it is hoped to collate in detail elsewhere. Trinomials are used only where essential.

The extent to which the various Palaearctic species move south in autumn shows extreme variation. Among those which travel an appreciable distance, some, like the linnet (*Carduelis cannabina*), reach the southern edge of the Palaearctic, as on the south shore of the Mediterranean, but go no farther. Others, like most of the waders (Limicolae) and the grey wagtail (*Motacilla cinerea*), winter extensively in both the Temperate Zone and the Tropics. Others, again, like the blackcap (*Sylvia atricapilla*), winter in the southern part of the Palaearctic and in the tropics. Finally, we have the long-distance migrants *par excellence*, exemplified by the swallow (*Hirundo rustica*), which leaves the Palaearctic completely, except for stragglers.

Table 1 shows approximately, by families, what Palaearctic birds migrate wholly or mainly out of the Palaearctic Region. Certain pelagic groups, e.g. auks and sea-

Table 1. *The systematic distribution of the chief long-distance Palaearctic migrants*

Family (1)	No. of Palaearctic breeding species (2)	No. of species leaving the Palaearctic Region wholly or mainly in winter (3)	Remarks on col. (3) (4)
NON-PASSERINES			
Grebes (Podicipitidae)	10	None	—
Herons (Ardeidae)	12	3	*Butorides striatus* and both *Ixobrychus* spp.
Storks (Ciconiidae)	2	2	—
Ducks and geese (Anatidae)	32	11	Practically all fresh-water ducks leave to some extent, but no geese or swans
Vultures (Aegypiidae)	3	None	—
Hawks (Falconidae)	43	27	Among the most typical migrants are insectivorous *Falco* spp. *Circus* spp., *Pernis apivorus* and *Butastur indicus*
Game-birds (Phasianidae)	22	1	*Coturnix*
Rails (Rallidae)	11	3	*Crex* and two of the *Porzana* spp.
Cranes (Balearicidae)	6	2	—
Waders (Charadriidae)	46	32	—
Snipe (Scolopacidae)	7	4	—
Gulls and terns (Laridae)	25	10	The fresh-water *Chlidonias* spp. especially leave completely
Pratincoles (Glareolidae)	2	2	—
Stone-curlews (Burhinidae)	1	1	—
Pigeons (Columbidae)	8	1	*Streptopelia turtur*
Cuckoos (Cuculidae)	5	5	—
Rollers (Coraciidae)	1	1	—
Kingfishers (Alcedinidae)	2	None	—
Bee-eaters (Meropidae)	2	2	—
Hoopoes (Upupidae)	1	1	—
Owls (Strigidae and Tytonidae)	15	2	*Otus scops* and *Asio flammeus*
Nightjars (Caprimulgidae)	3	3	—
Swifts (Micropodidae)	4	4	—
Woodpeckers (Picidae)	17	1	*Jynx torquilla*
PASSERINES			
Larks (Alaudidae)	13	1	*Calandrella brachydactyla*
Wagtails and pipits (Motacillidae)	12	8	—
Flycatchers (Muscicapidae)	12	12	—
Thrushes (Turdidae)	49	23	*Oenanthe* spp. and nightingales (*Luscinia* spp.) are among the most prominent migrants, *Turdus* spp. among the least
Hedge-sparrows (Prunellidae)	8	None	—
Wrens (Troglodytidae)	1	None	—
Dippers (Cinclidae)	2	None	—
Warblers (Sylviidae)	60	51	The exceptions are species which breed almost entirely in the southern part of the Palaearctic Region, especially the Mediterranean Basin
Swallows (Hirundinidae)	5	4	
Shrikes (Laniidae)	9	7	—
Waxwings (Bombycillidae)	2	None	—
Tree-creepers (Certhiidae)	2	None	—
Nuthatches (Sittidae)	4	None	—
Tits (Paridae)	24	None	—
Orioles (Oriolidae)	2	2	—
Starlings (Sturnidae)	6	4	—
Crows (Corvidae)	19	None	—
Weavers (Ploceidae)	9	None	—
Finches (Fringillidae)	38	None	—
Buntings (Emberizidae)	32	8	—
Total	589	238 (40% of the total)	

ducks, are omitted, as well as a few species which breed only on the extreme southern fringe of the Palaearctic. Among the land-birds, doubt arises for a number of species as to whether they should or should not be included in column 3 of the table, especially in the case of relatively ill-documented Far Eastern birds; but the general picture is certainly correct.

It will be seen that of the 589 species in Table 1, 238 wholly or mainly leave the Palaearctic Region in winter. Generally speaking, at least among the passerines, they are the most thoroughly insectivorous species; whether, like the flycatchers, they depend most on flying insects or, like the warblers, on soft-bodied insects found in foliage (e.g. larvae and aphides) or, like the roller, on large terrestrial insects. Within some other families (Phasianidae, Ardeidae) it is noticeable that the smallest members are the principal migrants; and this may in part result from the fact that the smaller body is less fitted to withstand cold.

As an example of the importance of migrant species in a Palaearctic avifauna, it may be noted that the British list of regularly breeding birds consists of about 180 species, fifty of which are wholly or mainly summer visitors. Of the seventy-six passerine species included in this total, twenty-two are species that winter almost entirely south of the Sahara and two others do so to a great extent.

GEOGRAPHY

The essential features of the geography of the Palaearctic migration system are conveniently summarized in the accompanying map (Fig. 1) on Mollweide's projection, which gives correct areas throughout, though the outlines of the land-masses are increasingly distorted towards the eastern edge of the map. For the present purpose the Palaearctic Region is taken to be much as Wallace (1859) outlined it many years ago, with its southern boundary at about 30° N., along the northern edge of the Sahara and across Arabia and Persia; bending north to exclude the Punjab, continuing along the south of the Himalayas and running at about 30° N. again across China and south of the Japanese islands. The total area of the Palaearctic Region is thus about 13 million square miles, of which about 3,750,000 are in Europe, i.e. west of about 60° E. But it is worth emphasizing that very little indeed of Africa (only the 'Horn of Africa', Somaliland) lies east of 40° E. This parallel runs through Archangel and the eastern end of the Black Sea; so that about one-third of Europe, as well as all Asia except Asia Minor and Syria, lies east of the bulk of Africa.

The potential wintering areas south of the Palaearctic may now be considered. The continent of Africa contains about 11·25 million square miles, but to arrive at the area habitable by birds it is necessary to deduct the Sahara, which in its extreme form has an average breadth from north to south of about 1000 miles and an area of about 3 million square miles. Over a great deal of that area bird life is impossible or is possible only for a few specialized forms. Excluding also the habitable portions of North Africa, totalling about 300,000 square miles, which belong to the Palaearctic Region, we arrive at a net figure of nearly 8 million square miles as the potential reception area for Palaearctic migrants in Africa.

Just to the east of Africa and due south of eastern Europe, the great land-mass of Arabia, totalling about 1 million square miles, is largely useless to birds on account of

its aridity. On the other hand, the great island of Madagascar, 250,000 square miles, appears ecologically suitable to support Palaearctic migrants, yet is almost entirely unvisited by any except 'waders' (Limicolae).

Much farther east lie the ecologically rich countries of India and Burma (together 1,800,000 square miles), subtropical China with Indo-China (together over 1 million square miles) and Malaysia and the Philippines (together 750,000 square miles). These 3·5 million square miles of southern Asia and its off-lying islands accommodate great numbers of Palaearctic birds in winter; but farther south New Guinea and Australasia are reached by hardly any except Limicolae.

Fig. 1. The eastern hemisphere on Mollweide's equal-area projection. The southern boundary of the Palaearctic Region is taken as following the parallel of 30° N. closely. The desert areas of Africa are shown dotted, the lowland evergreen forest areas are hatched.

It is useful for the present purpose to divide the Palaearctic Region longitudinally into a western section, due north of Africa, i.e. west of about 40° E., a central section, from there to the Yenesei (about 90° E., the longitude of the mouth of the Ganges), and a Far Eastern section, tapering from 90° E. to Bering Strait. In the Western Palaearctic thus defined we have about 3 million square miles opposite about 8 million square miles of potential winter-quarters on the other side of the Sahara. Moreover, the Western Palaearctic birds are favoured by the fact that much of the southern fringe of this section, in the Mediterranean Basin, has a better climate in winter than that of the same latitudes, both colder and more arid, in most of Asia. At the same time it should be noted, that south of the Mediterranean only the relatively small area of

300,000 square miles, the extreme southern fringe of the Western Palaearctic, is available before the desert begins.

By contrast with the Western Palaearctic, the Central Palaearctic (4·5 million square miles) has to the south of it much less habitable land-surface—little except India, say some 2 million square miles in all—which offers a genial winter climate. Also for the 5 million square miles of the Far Eastern Palaearctic only some 2 million square miles are available to the south. Actually the disparity between size of breeding area and size of potential wintering area for the birds of the Central and Far Eastern Palaearctic is not so important as the bare figures of areas would suggest, because in the great arid areas of Mongolia (the Gobi), Tibet, and Turkestan the density of the breeding population must be low.*

From the foregoing survey it might be expected that much of the movement of Palaearctic birds in autumn would be only generally southerly, with, on the whole, much westerly tendency. This tendency is familiar to us in Western Europe, though at the same time we are impressed with the well-marked south-easterly movement of certain species (such as orioles and shrikes). It is not so generally realized that for the huge area of the Central Palaearctic, from about 40° to 90° E., the biggest potential wintering area is Africa, which lies to the south-west; and that from most of the Far Eastern Palaearctic the birds must migrate south-west (not south) if they are to maintain any contact with land at all.

In considering the potential wintering areas it is important to recall the barriers which exist to the north of them. Western European birds have before them a crossing of the Mediterranean (which they make where the sea is broad as well as where it is narrow). Thereafter, and in all longitudes west of India, birds leaving the Palaearctic Region in winter are faced by the desert belt which stretches from the Atlantic to Mesopotamia and for over a thousand miles from north to south. This desert belt is too extreme to support migrant birds except in the Nile Valley and the few oases (see, for example, Moreau 1934). All these, including the Nile Valley, are exceedingly poor in habitats and relatively trifling in total area. Consequently, over at least half the Palaearctic Region migrants reaching its southern edge are faced, as it were, with a gigantic choice: they must either find winter-quarters north of the desert belt or push on for another thousand miles. The desert crossing, added, for many birds, to a Mediterranean crossing, is a source of heavy mortality; and that this solution of the problem of a winter habitat has been selected for so many populations of Palaearctic birds shows how impossible it would be for them to be accommodated in the Palaearctic Region for the winter.

In all, 183 species of birds regularly migrate, wholly or at least to some extent, from the Palaearctic Region to Africa south of the Sahara for the northern winter; and it is a remarkable fact, the reasons for which are not fully understood, that hardly any of them have been reported as remaining to breed in the south.

* Following Rübel (1930) or Good (1947) an area of Asiatic desert might have been depicted in Fig. 1. But it would have been somewhat misleading to do so because they use the same notation for the Asiatic arid area as for the Saharan; and the larger-scale (wall) map of Brockman-Jerosch entitled 'Die Vegetation der Erde' (Gotha, n.d., *c.* 1938) shows that the Asiatic desert belt is much more broken by patches of steppe and montane vegetation than the Saharan.

GEOGRAPHICAL DISTRIBUTION INTO WINTERING AREAS

As an indication of the way in which the birds of the several sections of the Palaearctic Region distribute themselves in winter it is convenient to analyse the passerines (which are uncomplicated by pelagic or shore-dwelling species) as shown below:

(*a*) *Western Palaearctic passerines* (*breeding north of the Mediterranean*)

	No. of species
Not migrating out of the Palaearctic	89
Wintering partly in the Palaearctic and partly in the Ethiopian Region	13
Wintering wholly in the Ethiopian Region	43
Wintering wholly in the Oriental Region	3
	148

A few species are, of course, not easily classified, but the general picture is clear. Of the Western Palaearctic passerines 29% find their winter-quarters wholly in Africa south of the Sahara and another 9% partly. If it is assumed that no populations would cross the Sahara as well as the Mediterranean unless it were necessary for their survival, it follows that over one-third of the Western Palaearctic passerine species depend on Africa for maintaining their status in Europe.

The three birds which breed in the Western Palaearctic (though only in the east and north-east of it) and winter exclusively in Asia are redbreasted flycatcher (*Muscicapa parva*) in India (Grote 1940), greenish warbler (*Phylloscopus trochiloides* (*viridanus*) in India, and Eversmann's warbler (*Ph. borealis*) in Indo-China and Malaysia (Ticehurst 1938). It is reasonable to suppose that these three remarkable migrations are due to a recent spread of the species from the east.

(*b*) *Central Palaearctic passerines*

Analysis here presents more difficulties. In the first place it seems reasonable to exclude from consideration the numerous species endemic and confined at all seasons to the Himalayas and neighbouring mountains. Then there are a number of species which have taxonomically indistinguishable populations breeding in both the Western and the Central Palaearctic, and which reach both Africa and India in the winter. Where relatively few individuals of such a species appear to reach India, while very large numbers of them reach Africa, it must be presumed that the latter are drawn largely from the Central Palaearctic and not all from the Western. On these lines we get the following analysis:

	No. of species
'Himalayan' (sedentary)	140
Others not migrating out of the Palaearctic	124
Wintering to some extent in India but not in Africa	37
Wintering in Africa but not in India	33
Wintering in both Africa and India	12
Wintering in south-east Asia	1
	207

Thus Africa provides winter-quarters for 22% of the Central Palaearctic passerine species against 24% which enter India, although India is so much nearer for them.

Africa exercises a special attraction for the shrikes (*Lanius* spp.) and the chats (*Oenanthe* spp.) of Central Asia, nearly all of which travel to Africa for the winter.

It is of interest to note also some of the non-passerine species which breed in the Central Palaearctic and: (i) winter in Africa but not in India—common crane (*Megalornis grus*), red-footed falcon (*Falco vespertinus*), black tern (*Chlidonias niger*), black-winged pratincole (*Glareola nordmanni*); (ii) winter abundantly in Africa and to some extent in India—demoiselle crane (*Anthropoides virgo*), Caspian plover (*Charadrius asiaticus*), great sand-plover (*Ch. leschenaulti* Lesson), Mongolian sand-dotterel (*Ch. mongolus* Pallas) and nightjar (*Caprimulgus europaeus*).

Cuculus poliocephalus Latham, which does not breed west of Tashkent, may be mentioned as a species of which some winter in Africa, while others, believed to be the majority, winter in southern Asia.

(*c*) *The Far Eastern Palaearctic birds*

The information available makes it difficult to analyse the Far Eastern avifauna in the same way as the above, to show the proportion which regularly migrates out of the Palaearctic Region. For the present purpose it suffices to point out that a number of species which breed as far east as Lake Baikal and beyond, even to Bering Strait, are known in the winter only in Africa (except for rare stragglers)—Amur falcon (*Falco amurensis*), *Megalornis grus*, *Caprimulgus europaeus*, common wheatear (*Oenanthe oenanthe*), pied wheatear (*Oe. leucomelas*), common rock-thrush (*Monticola saxatilis*), common redstart (*Phoenicurus phoenicurus*) and willow-warbler (*Phylloscopus trochilus*). The shortest distance that can be travelled by any of these birds between the Far Eastern Palaearctic and Africa is about 5000 miles and the most easterly populations of all, consisting of *Oenanthe oenanthe* and *Phylloscopus trochilus* must travel at least 7000 miles on each migration.

It is difficult to believe that at least some of these species would find it impossible to winter satisfactorily in south-east Asia or Malaysia. Shortage of suitable habitat or prevalence of competitors might be factors in preventing them from using potential winter-quarters that are geographically so much more obvious for these populations than Africa. There seems little doubt that at least some of them are deterred from entering India by the Himalayan barrier.

It is not my purpose here to discuss the routes by which Palaearctic birds reach their winter-quarters. There is, however, reason to believe that migration into Africa takes place irrespective of obstacles of sea or desert. Birds cross the Mediterranean in all longitudes; they cross the Red Sea and the Gulf of Aden throughout their length, presumably in flight between the Central Palaearctic and Africa; and a few long-winged species have been recorded in apparently direct flight nearly due west across the Indian Ocean towards East Africa (Moreau 1938). Most species do not seem to be restricted to narrow routes, but there are of course specific exceptions. Perhaps the most striking is the white stork (*Ciconia ciconia*), which has one extremely narrow concentration through the Levant and across the Gulf of Suez and another across the Straits of Gibraltar (cf. Rüppell 1942). Some species, such as the lesser spotted eagle (*Aquila pomarina* Brehm) and the sprosser nightingale (*Luscinia luscinia* (L.)), both breeding as far west as the Baltic, strike south-east across Europe so exclusively that they are

unknown in North Africa west of the Nile Valley. A few species, of which the best example is the golden oriole (*Oriolus oriolus*), have their main winter-quarters in the eastern half of Africa, and another wintering area, small and very isolated, in extreme western Africa. In such a case it can be postulated that in autumn most of the individuals breeding in Europe retrace the course of the species' original expansion westwards, while the most westerly breeding birds have pioneered 'rationally'-placed wintered quarters available to the south of them. A comparable process might have been expected in the Far Eastern birds mentioned in the preceding paragraph.

GEOGRAPHICAL DISTRIBUTION OF THE MIGRANTS IN AFRICA

In this respect there is the greatest variation. Some progress only a few degrees beyond the southern edge of the Sahara. At the other extreme, some species winter exclusively south of the equator. Yet others winter in all latitudes from the Sahara to the Cape. As will become evident from the ecological sketch of the Ethiopian Region in the next section of this paper, there is, except for some species in the first category of migrants (next paragraph) no obvious correlation between latitudinal distribution in winter-quarters and prevalence of habitat-type.

It is interesting to arrange the passerine migrants in the five categories which follow; but it must be emphasized that we do not always know the geographical limits of the main body of the species in winter and a few of the ranges may be fallaciously extended by records of stragglers.

(1) Species which winter little, if at all, further south than 10° N.:

Eastern calandra lark (*Melanocorypha calandra*) (Ménét.)
Short-toed lark (*Calandrella brachydactila*)
Blue rock-thrush (*Monticola solitarius* (L.))
Desert wheatear (*Oenanthe deserti*)
Black-eared wheatear (*Oe. hispanica*)
Song-thrush (*Turdus ericetorum*)
Ring-ousel (*Turdus torquatus*)
Stonechat (*Saxicola torquata*)
Black redstart (*Phoenicurus ochrurus*)
Bluethroat (*Cyanosylvia svecica*)
Orphean warbler (*Sylvia hortensis*)
Lesser whitethroat (*S. curruca*)
Rüppell's warbler (*S. cantillans*)
Desert warbler (*S. nana* (H. & E.))
Melodious warbler (*Hippolais polyglotta*)
Savi's warbler (*Locustella luscinioides*)
Bonelli's warbler (*Phylloscopus bonelli*)
Crag-martin (*Ptyonoprogne rupestris* (Scop.))
Great grey shrike (*Lanius excubitor*)
Nubian shrike (*L. nubicus*)
Cretzschmar's bunting (*Emberiza caesia*)
Ortolan bunting (*E. hortulana*)
Spanish sparrow (*Passer hispaniolensis* (Temm.))

Many of the species listed winter largely in the Palaearctic; and all those listed except the *Turdus* spp., the bluethroat, the lesser whitethroat and the great grey shrike are species which breed only in the southernmost part of the Palaearctic Region. A few species, the lark and the wheatears, breed in steppes so like the country on the southern fringe of the Sahara that they could hardly find any more congenial if they continued their journey further into Africa.

(2) Species wintering south to near the equator:

(*a*) Largely in the Palaearctic as well as south of the Sahara:

White wagtail (*Motacilla alba*)
Tawny pipit (*Anthus campestris*)
Chiffchaff (*Phylloscopus collybita*)

(*b*) Entirely south of the Sahara:

Woodchat shrike (*Lanius senator*)

(3) Species which winter mainly north of the equator (those marked † even to a considerable extent in the southern Palaearctic), but also regularly cross it to some extent. The latitudes in brackets show the approximate farthest south, all these limits being in Tanganyika Territory unless otherwise stated:

Red-throated pipit (*Anthus cervinus*† = *rufogularis*) (3° S.)
Pied flycatcher (*Muscicapa hypoleuca*), including *albicollis* (15° S., Northern Rhodesia and Nyasaland)
Common rock-thrush (*Monticola saxatilis*) (9° S.)
Pied wheatear (*Oenanthe leucomelas*) (6° S.)
Isabelline wheatear (*Oe. isabellina*) (6° S.)
Nightingale (*Luscinia megarhyncha*) (6° S.)
Blackcap (*Sylvia atricapilla*†) (15° S., Nyasaland)
Rufous warbler (*Erythropygia* (*Agrobates*) *galactotes*) (5° S.)
Upcher's warbler (*Hippolais languida*) (H. & E.) (4° S.)
Olivaceous warbler (*H. pallida*) (H. & E.) (5° S.)
Reed-warbler (*Acrocephalus scirpaceus*) (15° S., Nyasaland)
Isabelline shrike (*Lanius isabellinus*) (7° S.)

(4) Species wintering exclusively south of the equator, Kenya to South Africa unless otherwise stated:

Whitethroated robin (*Irania gutturalis* (Guér.)) (to 8° S. only*)
Luscinia luscinia (Kenya to Southern Rhodesia)
Olive-tree warbler (*Hippolais olivetorum* (Strickl.))
River-warbler (*Locustella fluviatilis*)
Basra reed-warbler (*Acrocephalus griseldis* (Hartl.)) (Kenya to Nyasaland)
Marsh-warbler (*A. palustris*)
Lesser grey shrike (*Lanius minor*)
Red-backed shrike (*L. collurio*)

(5) Species wintering in all latitudes from the Sudan and/or West Africa to South Africa:

Yellow wagtail (*Motacilla flava*)
Tree-pipit (*Anthus trivialis*)
Oenanthe oenanthe
Whinchat (*Saxicola rubetra*)
Spotted flycatcher (*Muscicapa striata*)
Common whitethroat (*Sylvia communis*)
Garden-warbler (*S. borin*)
Icterine warbler (*Hippolais icterina*)
Great reed-warbler (*Acrocephalus arundinaceus*)
Sedge-warbler (*A. schoenobaenus*)
Phylloscopus trochilus
Hirundo rustica
Sand-martin (*Riparia riparia*)
House-martin (*Delichon urbica*)
Oriolus oriolus.

Especially in view of the great area occupied by many of the species while in Africa, it might be expected that populations coming from different breeding areas would tend to be segregated; and the fact that so many of the species are represented in Africa by two or more subspecies would provide good material for detecting such segregation. It is, however, thoroughly well established that in nearly all these species, there is at least considerable overlap in the wintering ranges of the subspecies; and it does not seem likely that further study would reveal effective ecological segregation between them. On the other hand, there are a few cases of segregation of populations:

(*a*) In *Phylloscopus bonelli* and *Sylvia cantillans*, subspecies breeding in the east and the west respectively of the southern Palaearctic occupy corresponding parts of the semi-arid belt south of the Sahara in winter.

(*b*) For the swallow (*Hirundo rustica*) ringing has provided evidence for segregation on very unexpected lines (Schüz & Kuhk 1951). British breeding birds have been recovered almost exclusively in South Africa, while swallows from other breeding areas are nearly all retaken farther north. In particular, German birds winter much nearer the equator.

* But also in South Arabia, so it may be expected to turn up in Africa north of the equator.

(*c*) In a few, such as *Oriolus oriolus* and *Sylvia atricapilla*, which have their main winter-quarters in eastern Africa and another very limited area in extreme West Africa, the presumption is that the latter birds, which are 'morphologically' indistinguishable, are those which breed in extreme south-western Europe and in Barbary.

As already noted, the list of species wintering in the extreme north of the Ethiopian Region, between the Sahara and 10° N., consists partly of species which winter largely north of the Sahara, partly of birds which breed, as well as winter, in dry steppe. At the other distributional extreme are the species in category (5), which winter from the Sahara to South Africa. They include the two species with the most extensive breeding ranges of any in the Palaearctic, *Oenanthe oenanthe* and *Phylloscopus trochilus*; their total population, which drains out of 180 degrees of longitude into Africa, is enormous, and their wide spread in their winter-quarters becomes intelligible on those grounds. Similarly, *Hirundo rustica* (*rustica*), though breeding over less than half as big a range as the others, is known, by observation, to winter in very large numbers in many parts of Africa. But there is no such obvious reason why birds such as *Saxicola rubetra*, *Hippolais icterina* and *Oriolus oriolus*, certainly far less numerous than the foregoing, should be so widespread in winter.

Such considerations naturally suggest an attempt to compare, for various species, area of summer range with area of winter range, but it is thought that for most any result would, on present information, be fallacious; for such an investigation would need to take into account prevalence and continuity of preferred habitats in both summer and winter quarters, and also the real concentrations rather than the extreme recorded extensions of the birds concerned. Such critical data are lacking.

It is of some interest to compare different areas of Africa from the point of view of the number of Palaearctic species on their respective lists, in relation to their ecology and situation. The basis for the numbers of species is not altogether satisfactory, for it includes, for each area, those occurring in all degrees of prevalence; but that applies equally to all areas, and in any case attempts to subdivide the lists break down.

(1) West Africa (north of the Gulf of Guinea, but including Chad and British Cameroons; Bannerman 1930–51), well over 1 million square miles, excluding the evergreen forest, has sixty-six non-passerine species and thirty-seven passerine, compared with seventy and forty-three respectively in Kenya and Uganda, which together are less than half the size of West Africa. This result is attributable mainly to the number of Asiatic breeding species that enter East but not West Africa in winter. There is, however, also the fact that several species which breed due north of at least some part of West Africa as defined, or occur on migration in north-west Africa (Barbary), are, for no obvious ecological reason, unknown in West Africa—*Luscinia luscinia*, *Lanius collurio*, *Locustella luscinioides* and *Acrocephalus palustris*. Moreover, a number of other species which would be expected, on geographical grounds, to winter in West Africa abundantly, are unaccountably rare or local there (or both)—Montagu's harrier (*Circus pygargus*), jack snipe (*Lymnocryptes minima*), *Caprimulgus europaeus*, *Riparia riparia*, *Sylvia atricapilla* and *O. oriolus*. All these species occur in large numbers on the eastern side of the continent.

(2) The Belgian Congo has, as Chapin (1932) noted, but few more Palaearctic species on its list than South Africa, so much farther from the source of them. He

gave eighty-four species for the Congo compared with seventy-eight for South Africa, and attributed the result largely to the obstacle presented to migrants by the great block of equatorial forest (see map). A contributory cause may well be the absence from the Congo of the semi-arid or short-grass country which is preferred by some species.

AFRICA AS A WINTERING AREA

The wintering-period of the Palaearctic birds in Africa can, for purposes of discussion, be regarded as October to March inclusive, though some reach the tropics as early as August and many do not leave until April. During the migrants' stay different parts of Africa are subject to widely different climates, especially as regards the rainfall regime. Most of the area between the equator and the Sahara is already dry when the migrants arrive and it becomes drier as the winter proceeds. For except within about six degrees of the equator and especially in the semi-arid belt on the southern edge of the Sahara, the single rainy season comes to an end about August or September and not another drop falls until about May. On the other hand, in southern Africa, where the Palaearctic birds are present during the local summer, the rainy season (single south of about 6° S.) begins soon after their arrival and in the more favoured areas is not completely over when they depart.

Temperatures during the migrants' stay are high practically everywhere south of the Sahara. For example, five stations in the northern Sudan, the belt which includes Khartoum, have in January, the coolest winter month, mean maximum temperatures of 30·4–34·4° C. (87–94° F.) and mean minima of 10–16° C. (50–61° F.). Nearer the equator, as at Juba (4° 51′ N.), December–March is actually the hottest period of the year (being the farthest removed from the cooling effect of the rains), with mean monthly maxima varying between 36·0 and 37·9° C. (97 and 100° F.) and mean monthly minima between 19·7 and 21·7° C. (67 and 71° F.).

South of the equator the temperatures at the time of the migrants' arrival are in general the highest of the year. Thus, in Northern Rhodesia, at Livingstone and Broken Hill (17° 50′ S. and 14° 24′ S. respectively and both at altitudes over 2000 ft.) the mean maxima for October are 94·5 and 89° F. (mean minima 67° and 64° F.). At those two stations during the remainder of the migrants' stay the monthly mean maxima vary between 79 and 85° F. Much farther south of the equator the temperatures from October to March are still high. For example, at Johannesburg (26° 11′ S., 5750 ft.) the mean maxima vary from 76 to 80 °F., and at Durban (29° 52′ S., sea-level) from 75 to 82° F.

Detailed temperature comparisons would be out of place here, but it is clear that for a large proportion of at least North Palaearctic birds, the temperatures they encounter while they are wintering in Africa are higher than in their breeding area. No doubt, however, temperature is of far less direct importance to them than the vegetation types that Africa has to offer and their seasonal cycle.

Africa south of the Sahara consists, as we have seen, of nearly 8 million square miles. Of this, limited areas in south-western Africa and in the north-east (e.g. round Lake Rudolf) are, if not actually desert, so arid as to support little vegetation and few migrants. At the other extreme, some 750,000 square miles are covered with evergreen forest, mostly in the Congo Basin. By far the greater part of this is lowland forest,

which does not provide the main winter habitat for any Palaearctic species, except perhaps the honey buzzard (*Pernis apivorus*) on the edges. The other forest type, montane evergreen, attracts only a proportion of three wintering species, *Sylvia atricapilla*, *S. borin* and *Anthus trivialis*.

If we omit evergreen forest as well as desert as generally uninhabitable by Palaearctic migrants, we are left with about 7 million square miles of potential wintering area in Africa. This is clothed with a variety of deciduous vegetation, the description of which by Shantz & Marbut (1923), though imperfect, is still the most convenient. The ground cover, in its natural state, varies in different parts of tropical Africa from annual grasses and other ephemeral herbage to grass thickets 10 ft. high intermixed with woody herbage; the arborescent growth varies from a scattering of stunted thorny trees to thick clumps of semi-evergreen trees up to 30 or 40 ft. high and almost closed stands of *Brachystegia-Isoberlinia* woodland. Also, in all latitudes tropical Africa provides large areas of watery habitats, closed and open, fresh and brackish.

Knowledge of the habitats of Palaearctic migrants in winter is still defective. It can, however, be said that in general there is a broad resemblance between the type of the summer habitat and the type of the winter habitat. Thus, birds living in the foliage of trees and bushes in Europe do the same in Africa; nightingales (*Luscinia* spp.) seek dense thickets in Africa as they do in Europe. The common rock-thrush (*Monticola saxatilis*) and the wheatears (*Oenanthe* spp.), typically birds of the steppes, winter either in arid country, or if in more humid, in spots where the soil is bare, or even blackened by bush-fires. The shrikes also inhabit either arid country or, if more humid, spots where the ground is bare or covered with only short grass; in addition they need some perches a few inches or feet above the ground. Once such primary requirements are met, it seems, on our present imperfect evidence, that the Palaearctic species inhabit while in Africa a fairly wide range of climatic and vegetational conditions. No useful purpose would therefore be served by a detailed division or description of African vegetation types. Apart from the forest, which has already been briefly disposed of, it is however desirable to make one primary distinction, between semi-arid country and 'savanna'.

(*a*) *Semi-arid country* is dominated by small thorny trees and annual grasses. In the course of the dry season (which lasts up to 8 months continuously), the ground cover is so removed by wind and harvester termites that the surface becomes progressively more bare and dusty, until for a large part of the year the prevailing tone of the landscape is the colour of the soil. Such country occupies a strip (the Sudanese semi-arid), averaging 300 miles wide on the southern edge of the Sahara (cf. maps in Lynes 1924 and Bannerman 1930–51). It also occupies most of the country from the Gulf of Aden south through Somaliland and eastern Kenya, and much of south-western Africa. Lynes (1924) has given an impression of the Sudanese semi-arid belt, which Mr Peter Hogg of the Sudan Administration has been good enough to supplement for me (*in litt.*), and it appears that their accounts are applicable to most of the 1 million square miles of the semi-arid country that stretches from Dakar in Senegal to the Red Sea, with modifications in the immediate vicinity of the few rivers (mainly Niger and Nile). When all but the earliest migrants are arriving in autumn the ground vegetation is already dried up, grain crops are beginning to be reaped and wild seeds are dropped.

The insect population appears still to be high. Thereafter conditions steadily deteriorate; the ground gets barer and most of the trees lose their leaves. Not only is there no rain, but even dew fails to be deposited week after week. Away from the few great rivers, surface water is found only in the splashings from wells. In these circumstances the carrying-capacity of this semi-arid belt is amazing, for in addition to its far from poor resident fauna, it supports practically the whole wintering population of the following species throughout the winter:

Short-toed eagle (*Circaëtus gallicus* (Gmelin))
Turtle dove (*Streptopelia turtur*)
Tawny pipit (*Anthus campestris*)
Oenanthe deserti
Oe. hispanica
Monticola solitarius
Sylvia curruca (*curruca*)
S. hortensis
S. melanocephala
S. cantillans
S. rüppellii
S. nana
Phylloscopus bonelli
Lanius nubicus.

In addition, the Sudanese semi-arid belt supports a large proportion of the wintering scops owls (*Otus scops*), short-toed larks (*Calandrella brachydactila*), *Oenanthe oenanthe*, *Oe. isabellina*, *Monticola saxatilis*, *Emberiza hortulana* and *E. caesia*.

(*b*) *Savanna.* Country usually so called occupies most of tropical Africa. It is dominated by perennial grasses growing, according to the rainfall, up to several feet high, and its surface scattered with deciduous trees or with patches of thicket. It occurs in areas where the dry season is shorter than in the semi-arid—not longer than 6 months. During the growing period the cover is so tall and dense that most of the surface of the ground is inaccessible to birds, but as the dry season progresses the grass wilts and finally enormous areas are turned bare and black by bush-fires. With the increasing 'development' of tropical Africa, a larger proportion of the savanna country is being broken up for agriculture. The immediate result is to increase the amount of more or less bare land that would otherwise be covered for most of the year by the dense 'bush'. My observations and the frequent references in the literature show how generally many Palaearctic migrants appreciate artificial, 'garden', conditions.

The savanna belt north of the equator resembles the Sudanese semi-arid in that in most of it drought is progressive from the time the migrants arrive in the autumn. Southern Africa presents a striking contrast. There, October and November are the months witnessing the annual flush of vegetation and of the activity of nature in general (Moreau 1950). In the Cape Province of South Africa, this flush takes place well after the rains have begun, only when the weather has warmed up after the local winter. But over most of southern Africa, and most typically in the Rhodesias, the face of the country is transformed some weeks before the 6-months drought breaks, which is about November. By an astounding feat of plant physiology, well in advance of rain the savanna trees burst into leaf, and the ground, hard and blackened by fires, becomes pricked with green from the deep perennial root-stocks of the grasses. At the same time there is a flush of some kinds of insect food and most of the resident birds begin to breed. At this stage the immense immigrant population comes piling in on top of them, so that by the end of November, when the rains have everywhere broken, the food demands of both the resident species and the immigrants are at their maximum.

Within a few degrees of the equator the seasonal change in the aspect of the country is not so violent as it is farther south and farther north. The occurrence of two rainy

seasons in most parts of the equatorial belt, one about November–December, the other about April–May, means that the dry periods are not so severe. Conformably, there are two breeding seasons of the local birds, so that the annual fluctuations in numbers of residents must be smaller than at higher latitudes. But here again, when the Palaearctic migrants pour in (to East Africa in greater variety than anywhere else in the continent), it is during a breeding season, that of the 'short rains'.

THE POSSIBILITIES OF COMPETITION IN WINTER QUARTERS

At first sight it is surprising that so many immigrant species can be accommodated every year in an area that has so rich a resident avifauna—and this applies particularly to such a group as the shrikes (*Lanius* spp.), which are territorial outside the breeding season (cf. Simmons 1951; Verheyen 1951). Also, in such rigorous conditions as those of the Sudanese semi-arid belt, referred to above, it is *prima facie* astonishing that the numerous Palaearctic immigrants can live alongside the residents, especially in those groups (larks, doves and chats), some members of which are breeding there in the winter (Moreau 1950). It appears, however, that there may be ecological separation between the local breeding birds and their immigrant congeners (Hogg, *in litt.*); and the immigrants are not obviously more numerous than the local birds except along the few waterways. Nevertheless, the maintenance of so many immigrant birds alongside the residents in so desiccated a country presents an ecological problem that demands further study.

There is no exact information for any area about the relative numbers of local and Palaearctic birds present during the northern winter. Certainly the banks of the Nile and the Niger are not the only places where the immigrant birds are more numerous and conspicuous than the African. I found this noticeable also in January in parts of the Mbulu Highlands of Tanganyika (about 3° S.), which unwise use and subsequent erosion have reduced to poor grazing. Bushes and trees are confined to the occasional gullies and nesting sites are correspondingly limited. Pallid harriers (*Circus macrourus*), *Motacilla flava*, *Monticola saxatilis*, *Lanius collurio* and *Hirundo rustica* much outnumbered the native birds.

The European swallow, indeed, is a bird that has repeatedly been noted as locally outnumbering the resident hirundines, for example in part of the Congo (Ituri, Chapin 1932) and in South Africa, where four species are breeding at the time of its sojourn (cf. Taylor 1949). Also in South Africa Dr G. Rudebeck (*in litt.*) found the Palaearctic buzzard *Buteo b. vulpinus* "at least ten times as common" as the local *Buteo rufofuscus*. Again, on the shores of Lake Manyara (about 5° S.) Palaearctic waders are the most numerous birds for no less than eight months out of the twelve (Elliott & Fuggles-Couchman 1948).

There is undoubtedly wide variation in the type of ecological adjustment to be found among the Palaearctic birds during their stay. A form of interrelationship, which may occur frequently, is participation by migrants, together with resident birds, in mixed foraging parties consisting mainly of Muscicapidae, Sylviidae and Laniidae, as Winterbottom (1950) has noted of *Phylloscopus trochilus* in Northern Rhodesia. A few exploit, at least locally, niches which appear to have been left unoccupied by resident species, a position at first sight surprising in so rich an avifauna as the Ethiopian.

A conspicuous example is provided by the various subspecies of yellow wagtail (*Motacilla flava*), which, unlike any of the local passerines, accompany the herds of small stock to pasture and feed on the insects they disturb from the ground—with such regularity that in some native languages they are called the equivalent of 'herdsman'. Again, the pallid harrier, at least in parts of the East African highlands that I know, meets with no native raptor as it sweeps low over the open grassland. There are, too, localities where, unlike the eroded Mbulu highlands cited above, native birds are unaccountably scarce; and migrants fill their places. Thus in February on the north side of Kilimanjaro at about 6000 ft. there were no birds common in the clumps of semi-evergreen bush except blackcaps, garden warblers and the native bulbuls (*Pycnonotus xanthopygos* (H. & E.)). It is interesting also that I have in January found Tanganyika Forestry Department plantations of introduced *Cupressus* devoid of small birds except for willow-warblers (*Phylloscopus trochilus*).

At the opposite ecological extreme we have birds which seem inevitably to be sharing the niches and depending on the same food-supplies as the related native species among which they find themselves. For example:

(1) On a few hundred yards of road in Usambara (5° S.) we have collected in an hour after sunset specimens of two migrant nightjars, *Caprimulgus europaeus* and another species, *C. inornatus* Heuglin, which migrates south after breeding on the southern edge of the Sahara, as well as the locally resident *C. fossii* Hartlaub.

(2) In East Africa the grey wagtail (*Motacilla cinerea*) winters on the same mountain streams and appears to have exactly the same habits as the African *M. clara*.

(3) Both the snipes *Capella gallinago* and *C. media* winter in the patches of highland swamp where the Ethiopian snipe (*C. nigripennis* (Bonaparte)) is breeding (Guichard 1949, Elliott and Fuggles-Couchman 1948).

Whether in such cases actual competition occurs must depend on whether, contrary to appearances, these related birds in fact occupy different niches or whether food is temporarily super-abundant. Some species appear to pursue the latter conditions. The Palaearctic bee-eaters (*Merops* spp.) and swallows are conspicuously itinerant while they are in Africa, as all field-observers would agree. In South West Africa Hoesch & Niethammer (1940) have noted that great flocks of swallows descend on areas where the locally capricious rains of that dry land have induced a flush of ephemeral vegetation—and hence a flush of insects. White storks (*Ciconia ciconia*) follow locust swarms around—as for that matter does the African stork (*Sphenorhynchus abdimii* (Lichtenstein)). It would seem that in years when there are no actual locust outbreaks, and such years become commoner under the system of international locust control, the volume of food for these storks must be much less and the possibility of true competition for it increased. Similarly flocks of lesser kestrels (*Falco naumanni*), hobbies (*F. subbuteo*), Amur falcons (*F. amurensis*), and red-footed falcons (*F. vespertinus*) (often mixed) tend to concentrate where termites are emerging or locust-hoppers are available. No doubt the appearance of great numbers of lesser kestrels in Kenya and Uganda in January (Jackson & Sclater 1938) is a displacement of a similar nature on a bigger scale. Some passerines take part in similar movements, the immediate causes of which are quite unknown, in the middle of their stay in Africa; for marsh warblers (*Acrocephalus palustris*) used to come to the lighted windows of my house at Amani (5° 30′ S.) in January. This stood in a clearing on a forested plateau, so that the birds were presumably on a nocturnal migration of appreciable extent.

THE PAST

In the preceding sections an attempt has been made to present a picture of the present importance of Africa in the Palaearctic migration system and of the habitats that Africa can provide for the migrants. But it is worth while to stress that the state of affairs outlined above is purely temporary, for environments are always changing at both the northern and the southern ends of the system. Apart from any other factors, short-term climatic trends, extending over a few score years or a few centuries, continually succeed one another (Brooks 1949), influencing areas of various size in varying degrees, but most obviously at the higher latitudes. The extent to which the breeding ranges of Palaearctic birds can be affected by small changes, particularly of temperature, has recently been stressed, especially by Kalela (1949). Such alterations in the breeding range of a migrant species implies a change in its numbers, and that in most cases affects Africa.

(*a*) *The Tertiary*

Given areas in which there were marked seasonal changes in carrying capacity, we should expect migration to have existed since birds became capable of sustained flight, that is, since the late Secondary (Moreau 1952*a*). This means that the whole Tertiary is of potential interest to us in the present connexion. For our immediate purpose, a dominant fact is that, throughout the Tertiary, Africa existed in approximately its present size and shape. Moreover, there is geological evidence for various stages of the Tertiary that desert existed in at least some part of the Sahara and in the neighbourhood of the Kalahari. This is one of the reasons why I have accepted the view (Moreau 1952*b*), controverted by many, that throughout the Tertiary the equator, with its inseparable rain-belt, lay more or less where it does now, across the middle of Africa. If this view be correct, it follows that during most of the time during which birds have been capable of migration, Africa has provided about the same land-area and something like the present range of habitats. Only during the earlier Tertiary the coolest of the conditions now available in Africa, on the highest parts of the Tropics and in the extremity of South Africa, would have been absent.

In contrast to Africa, with its stable area and stable range of habitats, the other wintering areas and the Palaearctic Region itself have undergone immense vicissitudes. First, as to area: it was not until half-way through the Tertiary that Eurasia presented anything like the present continuous land-surface. North and east of Africa, from the North Sea to Malaya, with at one time an arm reaching across to the Arctic, was the Tethys Sea, of which the Mediterranean is a remnant. The land in the present Palaearctic area consisted of a number of islands, the Himalayan area had not yet risen above the waters of the Tethys, and India was an island consisting of the higher ground south of the present Ganges Valley (see, for example, Furon 1941).

The climate at this early stage of the Tertiary was much warmer at the higher latitudes than it is now; nevertheless, the winter nights would have been no shorter than they are now; and it is interesting to speculate what proportion of the birds on the Palaearctic islands had to migrate. It is worth recalling that the later Eocene of France contains, among others, fossils of *Numenius* and *Tringa* and the Oligocene of France *Anser*, *Tringa* (*Totanus*) and *Loxia*, alongside tropical genera, e.g. *Collocalia* and

Leptoptilos (Lambrecht 1933). The combination of crossbill, redshank and tropical swift suggests, what would be expected from the conditions just mentioned, that migration southwards may already have been taking place in the winter. Whether it crossed to Africa is only speculation, but there Africa was, offering a winter home. Moreover, the distance between the islands in the Tethys was not great and in particular the final gap at the proto-Straits of Gibraltar was always narrow (Furon 1941).

In the Miocene the shrinking of the Tethys Sea greatly increased the land area in the south-west of the Palaearctic. Later, the main changes took place on the shores of the Arctic and in south-east Asia, where in periods of marine regression the area of land greatly increased. As regards climate, that of the northern hemisphere in general was cooling, especially through the Pliocene, thus increasing the need for migration from the higher latitudes. Meanwhile, the increase in the Palaearctic land-area had multiplied the numbers of the birds that would take part in such a movement. Thus the demands of the Palaearctic for winter-quarters would have been increasing during the later Tertiary while the average sea-crossing to Africa was being progressively reduced by the shrinking of the Tethys. The demands made on Africa would have been the greater because by the Pliocene the Himalayas would already be a barrier to migration into India (which was then much the same size as now).

(*b*) *The Pleistocene*

The Pleistocene saw, of course, immense climatic fluctuations, which in Eurasia appear to have been more marked in the west than in the much drier and more 'continental' east. Corresponding fluctuations in the breeding populations of migrant species are certain, and coincident but smaller fluctuations took place in the capacity of Africa to support them in the winter.

At the maximum glaciation Europe was covered with a sheet of ice as far south as the Thames and the bend of the Don, about 50° N. Thence it swung north across eastern Russia to about 60° N. and, while there is wide disagreement about the limit of the ice in Asia, it is certain that a large proportion of Siberia north of that latitude was glaciated (Leuchs 1935; Bubnoff 1936; Gerasimov & Markov 1939). Also, south of this main polar ice most of the high mountains in Europe and Asia north of about 40° N. were glaciated, especially the Alpine area. Much of the Caspian Basin and of the western Siberian plains may at the same time have been flooded. Finally, south of the polar ice-cap, a great belt of country, across nearly the whole width of Eurasia, especially where loess was being deposited, had a poor climate, even in summer, dominated by dry winds from the north (see especially Zeuner 1937). A discussion of the vegetation zones at various stages of the Pleistocene would be out of place here; but for Europe it suffices to say that during a glaciation there was very little tree-growth north of a line drawn through the Pyrenees, the Alps and the south of the Crimea (cf. Büdel 1949). The last recurrence of this state was as recent as the last phase of the Würm glaciation, only about 25,000 years ago.

From the foregoing it is clear that in at least the Western and part of the Central Palaearctic the bird population during a glacial maximum can have amounted to no more than a third of what it was during the best of the interglacial or postglacial periods. In the long Mindel-Riss interglacial the climate was actually more genial than

at present. (Some elements of broad-leaf forest extended north as far as the White Sea (Gerasimov and Markov 1939).)

About the vegetational conditions of Asia at the glacial maxima and even about the number of maxima there, the latest information available shows wide disagreement. At one extreme Reinig (1937) has maintained that apart from the forest 'refuge' in Manchuria and northern China, almost the only parts of Palaearctic Asia which remained habitable by a land fauna were the treeless steppes of south-west Siberia and Turkestan. Previously, Tugarinov (1935), however, had held that parts of north-eastern Siberia had never been glaciated. Gerasimov & Markov (1939) have gone further, and argued that well away from the polar ice-cap conditions in Palaearctic Asia were comparatively stable throughout the Pleistocene, with a tendency to increased humidity in the south-west at a glacial maximum. In particular, the steppes east of the Caspian were less arid at the height of a glaciation owing to the southward diversion of the cyclone belt. It is thus difficult on the existing evidence to form so clear a conception, as was possible for Europe, of the effect of a glacial maximum on the numbers of Palaearctic migrants breeding in Asia, but the forested area would have been much reduced. If there was anything like as much highland ice in the middle of Asia as Leuchs and Reinig believed, then no birds from eastern Asia are likely to have reached Africa as they do now; and in any case there was the minimum inducement for them to seek winter-quarters in that direction because the land-surface of Malaysia was then at its greatest extent (see map in Mayr 1944).

It was at the glacial maxima, when the Palaearctic was making its lowest demands on Africa for winter-quarters, that Africa had the most to offer. For in the north the desert belt was much reduced in breadth, the mountains in the Sahara were well vegetated, rivers rising in those mountains ran in all directions and the inland-drainage basins held big swamps (Furon 1941, Moreau 1952*b*). In fact a large proportion of the present three million square miles of desert would have been habitable. On the other hand, but less important, it is at the glacial maxima that the tropical forest, a habitat not used by migrants, may have reached its greatest extension. The coincidence of the equatorial and the southern pluvials with the northern glaciations is, however, far from being established.

In any case, it is virtually certain that a far greater proportion of the Palaearctic migrants would have been able to winter in the northern half of Africa at a glacial maximum than at present. But it may be doubted whether all could do so. North of the reduced Sahara the winter climate would have been 'Mediterranean', cool and rainy, and immediately south of it very dry, as now; while south of the equator the rainy season beginning in October and November was, as now, producing the lusher conditions, rich in such insect food as flying termites and orthoptera.

The gradual and hesitant retreat of the ice to its present position in the last 25,000 years has opened a huge area for re-settlement by birds in at any rate the western half of the Palaearctic Region, and the demands made on Africa for winter-quarters have correspondingly increased. In Europe, the forest, re-emerging from its 'refuge' in the Mediterranean Basin, appears to have reached its maximum development in the warm, humid, 'Atlantic' phase, centred round about 6000 years ago, since when there have been minor fluctuations in the range of the different forest types (Firbas 1949).

But even since, with the disappearance of lowland ice from the Eurasian mainland, the essential conditions of the present state were reached, extensive changes have taken place in the details of the Palaearctic migration. Taking first the African end, there is little doubt that desiccation, degradation of vegetation and erosion have never been so widespread and severe as they are at present, largely as a result of more extensive, but ill-regulated, agricultural enterprise (cf. Jacks & Whyte 1939). This change is not altogether to the detriment of Africa as winter-quarters for birds; it involves the destruction of evergreen forest, the least acceptable habitat for migrants, and it increases the area of seasonally bare ground with early stages of regenerating 'bush', which many of them like. Any such advantage must, however, be out-weighed by the effects of the recent climatic trend, which has produced the present vast extent of the Sahara and the associated uselessness, through desiccation, of most of Arabia. The net result may well be that a larger proportion of Palaearctic migrants have to go farther south in Africa than ever before.

It may be noted incidentally that in Africa no crop-plant seems in itself to be of much importance to migrants, although, for example, willow-warblers may be seen 'working' infested cotton-plants (J. G. Williams *in litt.*). Yet an introduced weed, *Lantana camara*, has been noted as providing a favourite habitat for *Luscinia luscinia* in Southern Rhodesia (Smith 1951). A more significant concomitant of modern development is the erection of fences, poles and wires, which are appreciated by a variety of migrant species and permit them to utilize some areas of open country more than they otherwise could.

In at any rate the west of the Palaearctic, the changes in recent times have been far greater than in Africa. Europe was, except for the south-east corner of Russia, still dominated by forest at the time the Roman Empire was being established. From that time onwards, human factors, increasing agriculture, the demand for timber and firewood, over-grazing, have so reduced the forests and in places facilitated erosion that south of 60° N. Europe to-day carries only remnants of forest and those mainly coniferous, while stony, barren hillsides are prevalent in many parts. From the point of view of human economy the deterioration has been worst in the Iberian, Italian and Balkan peninsulas. (As an example of forest reduction in even an extremely mountainous area, the maps of Greece reproduced by Niethammer (1934) may be quoted.) But the ability of the land to support breeding birds, especially the long-distance summer migrants here considered, is probably nowhere lower than in extensive clean-farmed plains, a very recent development in ecological history.

As a consequence of the destruction of forest it would seem certain that in the last two or three thousand years the numbers of many woodland species needing winter-quarters in Africa must have been greatly reduced. Moreover, the areas of marsh in Europe at the dawn of history were vastly greater than now and were hardly touched by hunters, which meant correspondingly more storks, cranes, ducks, geese, rails, marsh terns and acrocephalines, as well as more waders, particularly ruffs (*Philomachus pugnax*).

Conversely, at the time of the European forest maximum the open-country habitats would have been restricted in area to an equivalent extent. Moreover, there were virtually no nesting sites provided, directly or indirectly, by man. These factors must

surely have meant a relatively small breeding population of several migrant species, for example kestrel (*Falco tinnunculus*), pallid harrier (*Circus macrourus*), quail (*Coturnix*), landrail (*Crex*), *Calandrella brachydactila*, *Motacilla flava*, *Anthus campestris*, *Oenanthe* spp., *Hirundo* spp. and house-martin (*Delichon urbica*).

Even during the last hundred years or so there have been important changes in the numbers of many migrant species. On the one hand there have been local avifaunal changes which can be correlated with the tendency for the climate of the north-western half of Europe to become more humid and equable and that of the south-eastern half to become more arid (Kalela 1949). On the other hand, human activity has changed the environment more rapidly than at any other time: farming and stock-raising have become cleaner and more intensive, marsh has been reclaimed on a bigger scale. Precision fire-arms and commercialized bird-catching have reduced the raptorial birds and some of the edible birds lower than ever before. It cannot be doubted that at the present time Africa has to accommodate in the winter far fewer marsh birds, wheatears, quails, raptors and probably swallows and martins now than a hundred years ago.

(*c*) *General*

It is evident from what has been said above that since the beginning of the Tertiary, and particularly since the beginning of the Pleistocene, very large fluctuations have taken place in the total numbers of Palaearctic birds requiring winter-quarters in Africa and also in the numbers of birds belonging to the various biotopes. The conditions offered by Africa appear to have been much more constant; so that the potential impact of Palaearctic birds upon the resident African birds must have varied greatly and mutual ecological adjustments in the past may at times have differed considerably from the present.

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SUMMARY

1. Migrants that leave the Palaearctic Region in winter are in the main the most insectivorous species. In Britain nearly one-third of the breeding passerine birds depend for winter-quarters on Africa south of the Sahara.

2. The Western Palaearctic has the potential wintering ground provided by tropical Africa, twice its own size, due south of it. On the other hand, the potential wintering grounds south of the Central and the Far Eastern Palaearctic are far smaller than these are. Consequently much of Palaearctic migration is directed south-west in autumn; Africa is sought by nearly as large a proportion of birds breeding in the Central as in the Western Palaearctic and even by some Far Eastern birds.

3. Some of the migrant species reaching Africa winter only north of the equator, some south, some throughout. Ecological reasons for these winter ranges are rarely obvious.

4. In most species populations breeding in different areas are not segregated in winter.

5. In the area between the Sahara and the equator the migrants arrive after the annual rains and experience increasing desiccation throughout their stay. Although few of the resident birds are breeding at that season it is surprising that so many immigrants can be supported under these severe conditions.

6. South of the equator the migrants arrive in time for the annual flush of vegetation, when the local birds are beginning to breed; so that both resident and immigrant populations reach their peak together—at the time of apparent maximum of food.

7. In some localities and in some genera the immigrant birds outnumber the residents.

8. Details of ecological adjustment in winter-quarters need to be worked out. Many immigrant birds appear to share a (possibly superabundant) food supply with allied resident species; some are highly itinerant. At least one species finds an unoccupied niche.

9. Africa has probably been an important wintering area since early in the Tertiary. The numbers involved varied most during the Pleistocene, with only one-third as many birds at a glacial maximum as during a climatic optimum. The post-glacial changes in the migrant flood have also been great, owing to the effects of human activity.

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THE POLECAT (*MUSTELA PUTORIUS*) IN WALES

By WILLIAM L. TAYLOR*

The British race of *Mustela putorius*, almost if not quite extinct in the English Counties away from the Welsh Marshes, and apparently nowadays equally scarce throughout Scotland, has proved remarkably successful in maintaining itself in Wales where the native stock has never quite been killed out in spite of persecution and the gin trap. The species has undoubtedly profited by the reduced intensity of game preservation since 1914 and may be said to have taken a new lease of life, and the opportunity to increase its range, in most parts of the Principality with the exception of the county of Anglesey. Occasion was taken in 1950 to obtain reports from the Forestry Commission's areas concerning the present status therein of this interesting survival among the members of our native Mustelidae, and from the resulting review of the position in the forests I am indebted to the willing co-operation of Mr A. P. Long, O.B.E., the Commissioners' Director of Forestry from Wales, and Messrs F. C. Best and W. D. Russell, Forest Conservators, and their resident Forester staffs.

Polecats were formerly sufficiently numerous in most parts of Great Britain to support an active trade in their pelts. Ritchie (1920) gives records of large numbers of polecat skins offered for sale in the south of Scotland in earlier years. But the polecat falls rather an easy victim to the steel trap and it is to this fact, and the apparently incurable tendency of gamekeeping interests to destroy all carnivorous species that come within their purview, that its disappearance from the greater part of Great Britain is due.

During the past two or three decades polecats have, from time to time, been reported from the island of Mull, in the Inner Hebrides, but specimens examined have been classified by zoologists as the progeny of escaped 'polecat' ferrets gone feral, or as crosses with the common ferret. Reports have also given indication that the polecat may continue to occur in parts of East Anglia and elsewhere. It is, however, only too clear that the last real stronghold of this native species is now in Wales.

Specimens measured and weighed by Mr Charles Elton, M.A., of the Oxford Bureau of Animal Population, whose help and encouragement I also gratefully acknowledge, vary from 374 to 425 mm. (body length) with tail length, to the end of the bones, from 123 to 140 mm., weights varying from 830 to 1160 g. The pelage shows considerable variation in coloration, in general being yellowish to cream with dark, sometimes almost black, guard hairs on the upper parts of the body and dark hair on the face and ears, legs and feet, and on the tail. In the Tregaron district of Cardiganshire a local race has developed a distinctly rufous coloration.

Formerly the polecat or foumart (in Welsh the ffwlbart) was frequently hunted with hounds. Several authorities testify that the species was still common in the first decades of the nineteenth century particularly in Wales and the Welsh border counties. Forrest (1899, p. 57) states that polecats were not rare in Shropshire in 1850 and also,

* Late Forestry Commissioner and Director-General, Forestry Commission.

at this period, that they were regularly hunted near Corwen in Merioneth. From 1850 onwards numbers diminished so rapidly as to evoke the statement that 'time cannot now be far distant when it will be as extinct locally as the marten'. Coward & Oldham (1910) tell us that polecats were common in the first half of the nineteenth century and states also (p. 357) that they had become extinct in Cheshire by 1900; they mention records from Delamere Forest up to 1883. Bolam (1913) reports polecats in fair numbers in south Wales and some to the north of the Dee valley. He says (p. 121) that 'Keepers are in the habit of following up their snow tracks and trapping'. Steel traps are given as the cause of extermination in Great Britain, also, in Wales, by reason of an influx of Scotch gamekeepers and their assiduous killing of all sorts of carnivores. Forest (1919) described the polecat as almost extinct in east Wales and Anglesey but not uncommon in parts of Caernarvon and Merioneth.

Matheson (1932) notes that the species appears to have increased in a remarkable way in Wales in recent years. In 1932 he considered the polecat to be very rare or extinct in industrialized Glamorganshire and Monmouthshire, though not uncommon half a century ago, but he records (Matheson 1937) the taking of a single specimen at St Fagans in 1934. Records supplied from an estate in central Wales show five polecats were trapped in 1928, sixteen in 1929, and eleven in 1930. On a single estate in the county of Brecknock, according to a report in the local press, nineteen were killed during the 12 months ending in May 1931, and definite records in his possession, from one source and another, indicate that approximately 230 polecats were destroyed in central Wales during the seasons 1929-32; from another estate that 130 were taken between 1928 and 1931; while, from yet another property, about ninety were killed during the same period—a total, admittedly incomplete, of 450 head. Matheson (1936) regarded the polecat as virtually extinct throughout Glamorganshire and notes that a hundred years earlier the species was so common that churchwardens in the county were paying bounties for those killed.

Reports received by Elton (personal communication) from Pest Officers of the Ministry of Agriculture and Fisheries in 1944 state that polecats were frequently being caught in rabbit traps in the counties of Radnor and Brecknock, twenty-five having been killed on one farm in 1943 (A. P. Hughes); also that they are 'plentiful' in Brecknock (J. Yule); a few in Cardigan (H. B. Heath) and in Montgomery (L. N. Davis).

In course of thirty years' explorations in the more remote parts of the Principality the writer has seen a number of polecats gibbeted in gamekeepers' 'larders' including, on one occasion in the early nineteen-twenties, five specimens at Cwmllecoediog in the Dovey valley.

Table 1 indicates the frequency or otherwise of the polecat in areas administered by the Forestry Commissioners during the three-year period 1947–50. The almost complete lack of positive records from the county of Brecknock is surprising but may be accounted for by the decrease in intensity of trapping consequent upon the reduction of rabbit populations in these forests.

Table 1. *Distribution of the polecat in Wales*

C, common; R, rare; 0, not recorded.

Forest	County		Trappings 1947–50	Forest	County		Trappings 1947–50
Newborough	Anglesey	0	—	Caio	Carmarthen	0	—
Beddgelert	Caernarvon	0	—	Crychan	Carmarthen	0	—
Gwydyr	Caernarvon	R	—	Brecon	Brecknock	0	—
Clocaenog	Denbigh	R	—	Coed Caerdydd	Brecknock	0	—
Coed Clwyd	Denbigh	R	—	Coed y Rhaiadr	Brecknock	0	—
St Asaph	Flint	0	—	Halfway	Brecknock	0	—
Hafod Fawr	Merioneth	R	—	Glasfynydd	Brecknock	0	—
Cynwyd	Merioneth	0	—	Hay	Brecknock	0	—
Coed y Brenin	Merioneth	R	—	Mynydd Ddu	Brecknock	0	—
Aberhirnant	Merioneth	C	12	Usk	Brecknock	C	—
Dovey	Merioneth	C	—	Monmouth	Monmouth	C	2†
Dovey (Corris)	Merioneth	C	3	Tintern, north	Monmouth	C	1
Dyfnant	Montgomery	C	2	Tintern, central	Monmouth	R	—
Carno	Montgomery	0*	—	Tintern, south	Monmouth	0	—
Bryncynfil	Montgomery	C	—	Itton	Monmouth	R	—
Commins Coch	Montgomery	C	2	Chepstow	Monmouth	0	—
Hafren	Montgomery	C	2	Goytre	Monmouth	C	—
Kerry	Montgomery	C	4	Llanover	Monmouth	0	—
Mathrafel	Montgomery	R	2	Hencol	Glamorgan	0	—
Tarenig	Cardigan	C	4	Llantrisant	Glamorgan	0	—
Myherin	Cardigan	C	—	Margam	Glamorgan	0	—
Cwmeinion	Cardigan	R	—	Penllegaer	Glamorgan	0	—
Brynmawr	Cardigan	C	4	Rheola	Glamorgan	0	—
Radnor	Radnor	R	1	Slebech	Pembroke	0	—
Coed Sarnan	Radnor	R	—	Coed y Gocor	Shropshire	R	1
Brechfa	Carmarthen	R	—				

* Believed to be present.

† 12 also killed on nearby property during the period.

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THE INFLUENCE OF LIGHT AND OTHER FACTORS ON THE SEAWARD MIGRATION OF THE SILVER EEL (*ANGUILLA ANGUILLA* L.)

By ROSEMARY H. LOWE

*East African Fisheries Research Laboratory, Jinja, Uganda**

(With 13 Figures in the Text)

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INTRODUCTION

The silver eel represents a phase in the life-history of the European eel, *Anguilla anguilla* L. In 1894, C. G. J. Petersen showed that this eel lives and feeds in fresh water as the yellow-bellied 'yellow' eel and changes to the silver form when about to migrate to the sea to spawn. In 1906, Petersen recorded that it was well known among fishermen that the silver eels migrate downstream almost entirely by night and on nights when the moon is not shining in the evenings. The light-shyness of the silver eel may be correlated with the increase in the size of the eye which characterizes the change from the yellow to silver form and is part of the preparation for the journey at great depth to the Sargasso Sea. Petersen also carried out some experiments on the use of light to check the migration and attempted to deflect eels into traps with light. The results of these experiments were promising. They showed that the migration could be checked by artificial light but that more experiments and further knowledge of the behaviour of the migrating eels was required before lights could be used to deflect eels into traps.

Britain imported from the continent as food about 2000–3000 tons of live eels each year in the years before 1939. The cessation of this supply in 1939 and the need for

* Formerly on the staff of the Freshwater Biological Association, Ambleside, Westmorland.

home-produced foods during the war provided an impetus to the development of British eel fisheries. Fresh-water eels are most easily trapped in large numbers when migrating seawards, but they travel during autumn floods when traps and eel weirs become blocked with flood debris; this reduces the efficiency of the traps and may cause flooding of the neighbouring land. Experiments were therefore carried out by the Freshwater Biological Association in co-operation with the Ministry of Agriculture and Fisheries on the possibility of deflecting eels by means of artificial light into traps placed at the side of a river away from the main stream and flood debris. These experiments, made during 1941–4, and observations made at the same time on the conditions under which silver eels migrate, are described in this paper.

Fishermen state that silver eels 'run' on certain nights. Throughout this paper a 'run' of eels means the number migrating on any one night. One of the experimental traps, at Dalemain on the River Eamont, which catches almost all the eels migrating from a catchment area of about 76 square miles, was fished day and night throughout the year for 2 years; catches confirmed that the runs of silver eels were all at night and were confined to the late summer, autumn and early winter months.

An attempt was made to discover what conditions limit the migration to certain nights, what initiates the migration and how the eels are guided seaward. The migration was considered from four aspects:

(1) The physiological preparation; this is indicated by the change from the feeding yellow eel to the migrating silver form but is not discussed in this paper.

(2) Some external condition or conditions may act as a trigger and start the downstream migration; whether an eel is ready to migrate immediately it has become silver or has to be stirred to activity by external conditions is considered here.

(3) Possible directional factors guiding the eel to the sea are considered.

(4) The run is checked during the day and often for longer periods; whether these checks are caused by the inhibiting effect of some factor such as light, or the absence of excitatory stimuli is discussed.

Although the fishermen have considerable knowledge of conditions associated with silver eel migrations, the published accounts (e.g. Petersen 1906; Bertin 1942) only state that runs occur on dark nights and in floods, and make little attempt to analyse the conditions. Also, although the silver eels' avoidance of light has been exploited in eel fisheries in several countries for many years the only experiments on the light reactions of eels appear to be those of Petersen (1906) and Cox (1916). The observations recorded here were discontinued in 1945; there has been an unavoidable delay in publishing the results but no other work on the light reactions of eels has been published in the intervening years*, though Frost (1950) has considered the factors influencing the seaward migration of silver eels in the River Bann, Northern Ireland.

Petersen (1906) mentioned that in the big eel fisheries on the Italian lagoons at Comacchio bonfires are sometimes lighted to check the run of eels while the nets are emptied and reset. According to Bertin (1942) these bonfires at Comacchio are lighted to 'calm' the eels in the traps when their struggles are so great that the fishermen fear they will break the traps. Reports from Irish rivers (Frost, personal communication; Went 1944) tell of blazing turfs placed to check the run of eels while the nets are

* See note on p. 309.

emptied. In 1904–6 Petersen, working in Danish waters, found that by turning a light projector on or off he could prevent or allow silver eels to migrate through a sluice into a trap fixed below it. Petersen also tried underwater lights, but owing to a poor run of eels no results were obtained; he also suggested throwing light obliquely on to the water surface to drive eels into nets set deeply to avoid interference with navigation. In his paper Petersen expressed the hope that further experiments would be carried out by fishermen with eel fishing rights, but no reports of subsequent work have reached this country. Cox (1916) tried the effect of acetylene lamps on the Canadian eel, *Anguilla chrysypa* Rafinesque-Schmalz (now considered to be a synonym for *A. rostrata* (Le Sueur)), in its feeding phase in an attempt to stop it running upstream into fish-spawning grounds. Cox concluded that although the eels were afraid of the light it seemed unlikely that their ascent could be arrested by such means.

The experiments described in this paper were originally concerned with the possibility of deflecting eels by light but confirmation of the effect of lights in stopping the run was obtained. These confirmatory results are recorded as Petersen's experiments were of a preliminary nature only and did not give much information on the conditions of the eel run and light intensities, etc., which stopped the run. Results recorded here are not all in chronological order as observations on the effect of light in stopping the run arose out of attempts to deflect the eels.

As positive results from experiments with light might have had immediate application, early trials were made in the field on a fairly large scale, as well as in still-water tanks in the laboratory at Wray Castle by Miss M. E. Brown. In 1941 the field trials were made at four sites: (1)* on the Cunsey Beck, the 8 yd. wide stream which drains Esthwaite Water into Windermere and an ideal experimental site since the whole width of the stream could be fished; (2)† on the River Leven flowing from Windermere, at Newby Bridge where the river is about 70 yd. wide; (3) Backbarrow 2 miles farther down the River Leven; and (4) at Spark Bridge on the River Crake which flows from Coniston Water.

The eel runs in 1941 were very poor, few eels were caught during lighting experiments on the three last-named sites, and as much damage was done to the gear experiments at these sites were discontinued. On the Cunsey Beck, however, significant results were obtained, so in 1942 further experiments were made on this stream and at three other field sites, Nibthwaite, Dalemain and Corby Castle, chosen as they provided diverse conditions which might be typical of eel traps in other parts of the country. It is with the results of these 1942 experiments and those made on the Cunsey Beck in 1943 and 1944 and in a specially constructed artificial river in the laboratory that this paper is concerned.

FIELD OBSERVATIONS

(*a*) *Methods*

Observations were made at six field sites (Fig. 1) on the numbers of eels migrating, the water-level, darkness of the night and general weather conditions, from the start

* These experiments were carried out by the Freshwater Biological Association's staff under the direction of Dr E. B. Worthington.

† Mr M. Graham of the Ministry of Agriculture and Fisheries staff was in charge of this large-scale experiment at Newby Bridge, together with subsidiary experiments at Backbarrow and Spark Bridge.

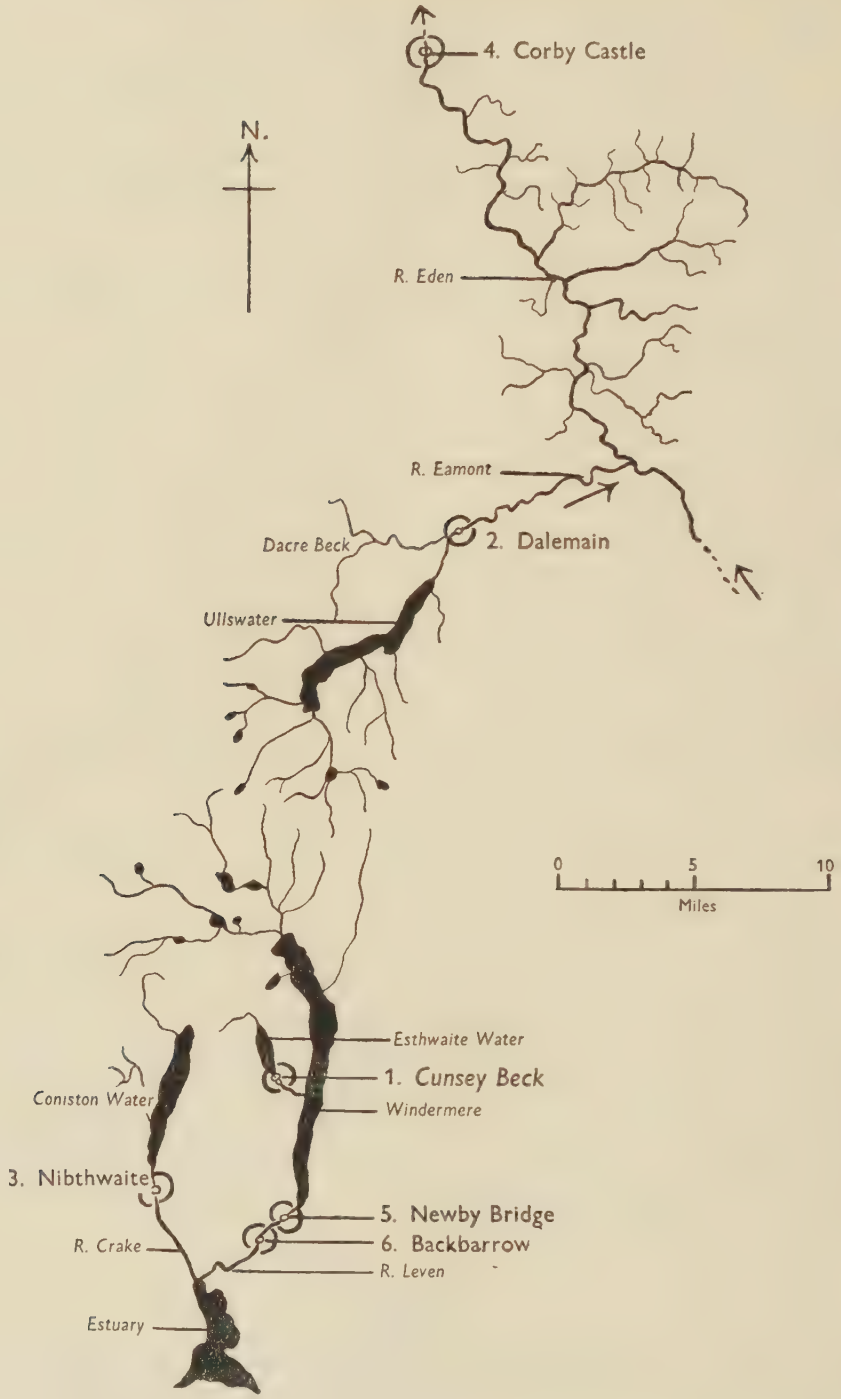

Fig. 1. Map showing the sites of the eel traps at which observations were made.

of the autumn migration (about July) until the migration ceased. At four of these sites the responses of migrating eels to artificial lights were tested. During these experiments the eel traps were watched throughout the night and more detailed observations made on the eel runs. These sites were:

(1) On the Cunsey Beck, the eel trap was situated near the outflow from Esthwaite (Nat. grid ref. 34/366952) in 1941–4. This trap gave the most reliable records, as the whole width of the beck was fished continuously day and night from about July to November in these years. This was the main site for experimental work on the light reactions of eels so the traps were watched throughout the nights on which the eels were migrating in any number, and information was obtained on the time of night at which the eels were caught, and also on the prevailing conditions such as water temperature, weather and darkness of the night. The 'darkness' was estimated by means of a modified 'Secchi disk' used in air, and measured by the horizontal distance at which four white circles, 3 in. in diameter on a black background, first appeared distinct when approached, the same individual taking these readings throughout the season. In 1941 and 1942 a second pair of traps were placed on top of the others at this site when the water was high; this gave information on the depth at which the eels were swimming.

Attempts were made, using baited and unbaited traps, fyke nets and seines, in Esthwaite Water to see whether silver eels congregate near the outflow of the lake and there await conditions suitable for the downstream migration. Attempts were also made to create artificial runs of eels down the Cunsey Beck, using silver eels trapped in the eel trap on this site and stored in live boxes in the beck. Batches of ten silver eels were moved by day and dark-adapted in boxes floating in the beck about 6 yd. above the eel trap. At night the trap was fished for some hours to see whether any natural run occurred, and the dark-adapted eels were then released.

In an attempt to estimate the speed at which the silver eels moved through Esthwaite fifty-seven eels trapped in the Cunsey Beck on 8–9 August 1943 were marked by clips fastened through the tail in three different ways, and the three batches of eels were returned to Esthwaite the same day, nineteen to the top end of the lake $2\frac{1}{2}$ miles from the trap, twenty half-way down the lake four-fifths of a mile from the Cunsey Beck and eighteen near the south end of Esthwaite 520 yd. from the Cunsey Beck outflow. All the eels when released in the lake were active and swam away quite normally.

(2) At Dalemain on the River Eamont just below the inflow of Dacre Beck and about 2 miles below the source of the river in Ullswater, a large commercial eel trap is situated (Nat. grid ref. 35/482268). Except in high water, almost all the eels migrating downstream are deflected into this trap by the 60 yd. concrete weir constructed for this purpose. This is the trap which was fished throughout the year for 2 years to find whether eels migrate at times of year other than the autumn. During 1942 when lighting experiments were in progress here more detailed records were kept.

(3) At Nibthwaite, on the River Crake about 2 miles below its outflow from Coniston Water (Nat. grid ref. 34/294884), records were kept in 1942 and 1944 of catches from a commercial trap leading from a mill leat back to the river. More detailed records were kept here in 1942 when light experiments were in progress. As only a small part of the width of the river was fished, catches at this site have only

relative significance as there would be some variation in the proportion of the migrating eels trapped.

(4) Records of catches were made at Corby Castle on the River Eden (Nat. grid ref. 35/468538) when lighting experiments were in progress in 1942. Here again only a small part of the river was fished and few eels were taken. The main interest here

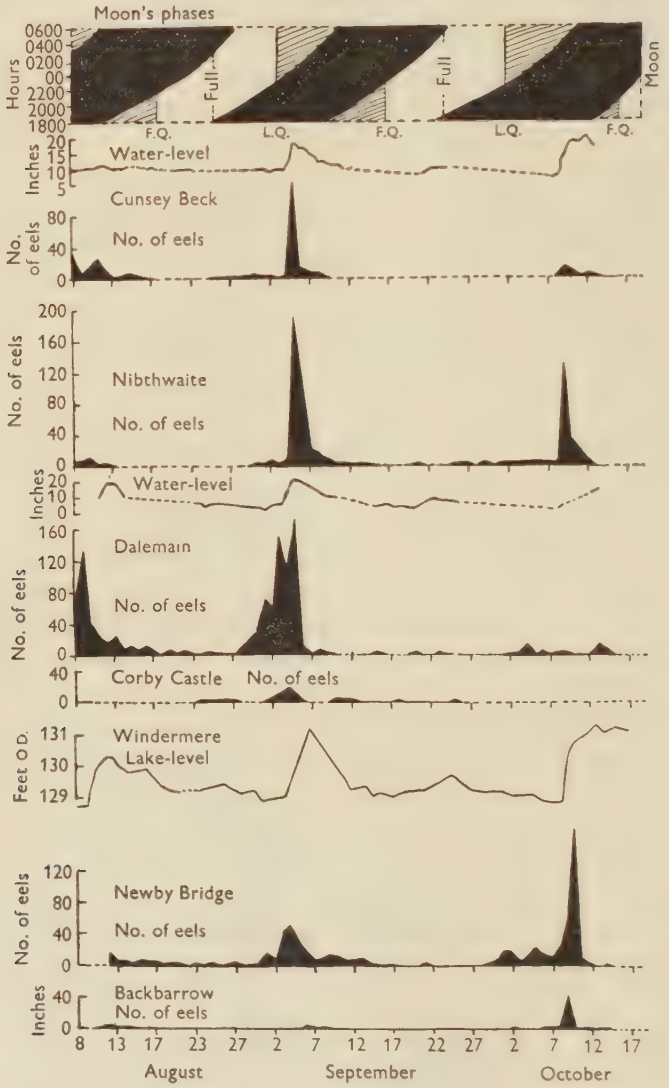

Fig. 2. Eel runs in 1942 in relation to the phases of the moon and floods.

was comparison of the eels' behaviour with that at other sites, as this site was far from any lake.

(5 and 6) Records of catches were also kept by two eel fishermen under the guidance of Dr W. E. Frost of the Freshwater Biological Association's staff, at two commercial eel traps on the River Leven. The more productive of these traps was at Newby Bridge, where the River Leven leaves Windermere (Nat. grid ref. 34 368863); this trap fished the water from a mill leat as it flowed back to the main river. As the amount

of water flowing through the trap varied there would be some variation in the proportion of the migrating eels which were trapped. In spite of this source of error the fluctuations in the numbers of eels caught were so marked that the results were still of value. The second trap was at Backbarrow about 2 miles farther down the River Leven (Nat. grid ref. 34 358849). This trap also fished water from a mill leat only, and as the leat led from the right bank and the main rush of water in the river was nearer the opposite bank few eels were caught. In addition, catches at this site were influenced by the Newby Bridge trap up river, and the trap was tampered with on several occasions.

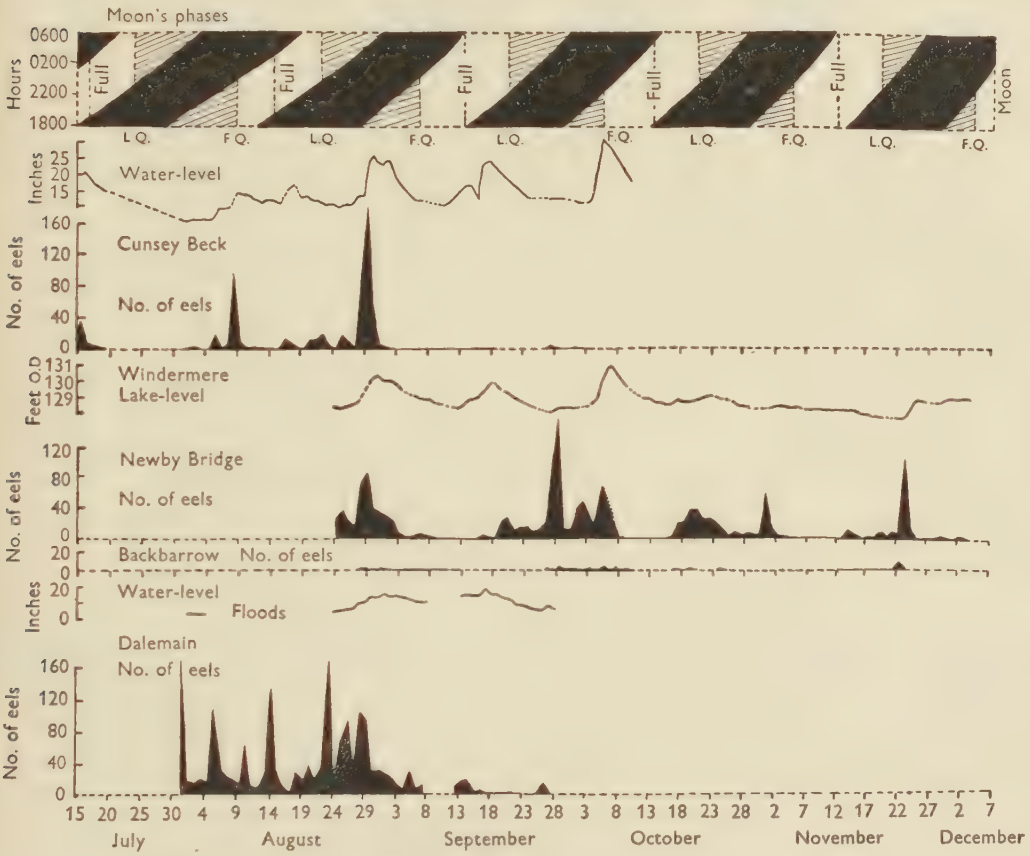

Fig. 3. Eel runs in 1943 in relation to the phases of the moon and floods.

(*b*) *Results*

Eels migrated on very few nights during the season, and on these few nights large numbers of eels migrated. Since the peak runs occurred on the same nights at all sites the conditions determining whether the eels migrate or not must be uniform over the whole district. This was particularly marked in 1942. The nightly totals of eels caught at the various sites are given in Figs. 2–4 for the years 1942, 1943 and 1944. The water-level and moonlit hours of the night are also shown.

The major peaks in numbers of eels migrating occurred when floods happened to coincide with moonless periods. When a flood coincided with a full moon, the run of

Table 1. *Numbers of eels caught during each lunar month, the dates being those of full moon*

(Figures in brackets are calculated or partly calculated.)

	Sites on rivers draining into the River Leven				Other sites	
	Cunsey Beck	Nibthwaite	Newby Bridge	Backbarrow	Dalemain	Corby
Miles from the sea...	10	4	3	1	50	15
1942						
28 July–26 Aug.	110	45	73	5	(625)	3
27 Aug.–24 Sept.	145	343	(278)	12	639	73
25 Sept.–24 Oct.	29	210	(389)	59	57	1
25 Oct.–22 Nov.	0	1	37	8	1	—
23 Nov.–22 Dec.	0	0	16	0	0	—
Total	284	599	(793)	84	(1322)	77
1943						
6 June–17 July	49	—	—	—	(94)	—
18 July–15 Aug.	173	—	—	—	(771)	—
16 Aug.–14 Sept.	443	—	407	12	(1005)	—
15 Sept.–13 Oct.	21	—	(610)	19	55	—
14 Oct.–12 Nov.	0	—	295	6	0	—
12 Nov.–11 Dec.	—	—	175	13	0	—
Total	686	—	(1487)	50	(1925)	—
1944						
6 June–6 July	1	—	—	—	38	—
7 July–4 Aug.	1	—	58	—	121	—
5 Aug.–2 Sept.	116	150	575	2	604	—
3 Sept.–2 Oct.	204	191	534	14	295	—
2 Oct.–31 Oct.	79	130	843	177	28	—
1 Nov.–30 Nov.	—	—	—	9	—	—
Total	401	471	2010	202	1136	—

Table 2. *Weather conditions at Cunsey Beck on nights when over thirty eels were trapped*

Date of first part of night	No. of eels	Water-level (in.)		Water temperature (° C.)		Conditions during night			Visibility of 'Secchi disk' (feet)
		At start of run	Following day	Previous day	Actual day	Rain	Wind	Cloud	
1942									
8 Aug.	33	11	12	—	—	No rain	—	6/8, few stars	—
11 Aug.	37	14·5	15	—	—	Slight drizzle	Gusty	8/8, overcast	—
5 Sept.	123	27·5	24·5	16·3	15·8	Very slight drizzle	—	3/8, few stars	—
1943									
15 July	35	20·5	20·5	—	—	—	—	—	—
8 Aug.	96	14·5	14	17·9	17·2	Fine very slight rain	Windy	8/8	27
28 Aug.	89	13·5	19·5	16·5	15·9	Faint drizzle at intervals	No wind	6/8, few stars	45
29 Aug.	185	19·5	26	—	15·6	Heavy rain	Gusty	8/8	25
30 Aug.	53	26	23·5	—	15·1	Fine	No wind	3/8, stars	25
1944									
28 Aug.	106	11	9·5	—	—	No rain	Slight, N.W.	6/8, no stars	42
6 Sept.	69	18	16·5	14·5	14·5	Heavy rain	—	8/8	—
15 Sept.	38	5	8	—	13·6	Heavy rain at intervals	Gusty, S.W.	8/8	13
11 Sept.	44	6	10·5	11·6	11·8	Slight drizzle	Gusty	8/8	14

Table 3. *The depth at which the eels were swimming in the Cunsey Beck*

	1941	1942
Eels taken in upper 1 ft. 6 in. of water	14	17
Eels taken in bottom 1 ft. 6 in. of water	28	148
Significance (P)	0·045*	0·0002**

The symbol * is used to indicate 'significant' ($P < 0{\cdot}05$); ** indicates 'highly significant' ($P < 0{\cdot}01$); absence of any symbol indicates 'not significant'.

eels was generally delayed, as at Cunsey Beck in September 1944 and at Newby Bridge in October 1944. On the other hand, at Dalemain in August 1943 and September 1944 the eels continued to run throughout the full moon period; the water flowing down the Dacre Beck is very turbid in floods but this would not affect the eels migrating from the lake. A run may occur without a flood at the dark of the moon. This happened in 1942 at Dalemain and at Nibthwaite in early September, when there had been no flood for many days, and at Newby Bridge in early October. It also happened in August

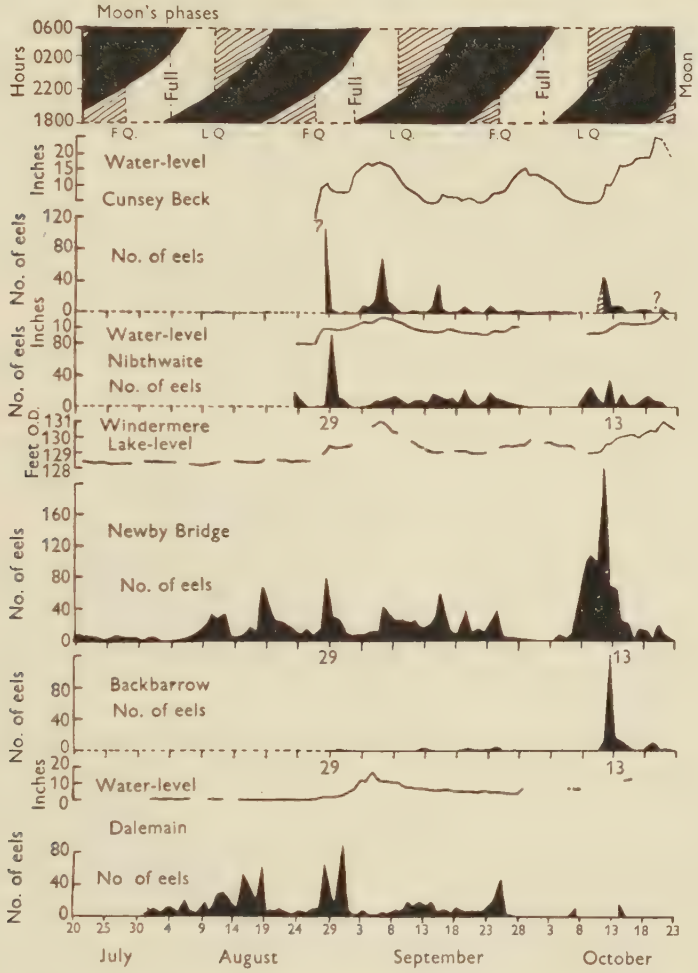

Fig. 4. Eel runs in 1944 in relation to the phases of the moon and floods.

1943 at Cunsey Beck and in August, September and October 1944 at Newby Bridge. In all these cases the numbers of eels concerned was relatively small, a peak run occurring when the flood came. The greatest catches were made in rising floods, and catches fell off on subsequent nights even when the river remained at a high level.

The higher upstream, the earlier in the season the eels were trapped. This is as would be expected and demonstrates the passage of the eels through the drainage area. Figs. 2–4 show that the majority of eels are caught earlier in the season in Cunsey Beck, which flows into Windermere, than at Newby Bridge and Backbarrow on the River

Leven, flowing from Windermere. The Dalemain trap, which is about 50 miles from the sea, has an earlier eel season than have the Newby Bridge or Nibthwaite traps which are only 5 or 6 miles from the sea. This is also brought out by the figures for the number of eels taken at various sites for periods between one full moon and the next (Table 1).

During the autumn the water temperature is likely to be falling almost continuously and records of water temperatures from Cunsey Beck (Table 2) and from Windermere indicate that a fall in temperature was associated with each large flood. Weather conditions during the early hours of the night did not seem as important as changes in water-level in determining whether the eels would migrate or not. This is clear from the records from Cunsey Beck (Table 2) concerning rain, wind, cloudiness and visibility.

At Cunsey Beck in 1941 and 1942 two traps were fished one above the other when the height of the water allowed, thereby distinguishing between eels swimming in the bottom 18 in. and surface water. Results for the 2 years are shown in Table 3. The 1941 figures suggested that 33% of the eels were swimming in the surface water, and in 1942, 10%; the difference was statistically significant in both years ($P = 0{\cdot}045$ in 1941 and $P = 0{\cdot}0002$ in 1942).

Table 4. *The time of night of migration during the four nights at Cunsey Beck in* 1943 *when over fifty eels were caught*

	Range of water level (in.)	Time at which fishing started (G.M.T.)	Hours of fishing								Rest of night	Night's total
			1	2	3	4	5	6	7	8		
8–9 Aug.	14·5–15·5	2125	16	23	23	21	11	2	0	0	0	96
28–29 Aug.	13·5–14·5	2040	2	11	15	25	19	14	1	1	0	88
29–30 Aug.	19·5–24·5	2036	27	38	28	37	19	15	13	3	1	181
30–31 Aug.	26–24	2037*	14	17	13	4	2	—	—	—	3	55

* 2 eels caught earlier.

At Cunsey Beck, Dalemain and Nibthwaite eels tended to migrate in the early hours of the night except on a strongly rising flood. At the Cunsey Beck trap the eels generally arrived immediately it was dark. Corby Castle, unlike the other three sites, is not near the outflow of a lake, but here too the few eels which were caught came early in the night on a rising flood. On nights when the rivers were rising rapidly the migration might start during the night and be accelerated towards morning. Table 4 and Fig. 5 (*b–d*) show the results for three consecutive nights of a 'migration period' at Cunsey Beck, and it is clear that the peak rate of catch was earlier on each successive night, being immediately after dark on the third night.

During attempts to see whether silver eels congregate near the outflow at Esthwaite Water no fully silver eels were taken, either near the lake outflow or on reputedly good eel ground fished as a control farther up the lake. Seine nettings across the whole width of the lake above the outflow were made at dusk on 28 August 1944 but no eels were caught, even though the Cunsey Beck traps 100 yd. downstream caught four fully silver eels while the netting was in progress.

(*c*) *Experiments with marked eels*

Only fourteen out of forty silver eels returned to the Cunsey Beck 60 yd. above the traps were retrapped the same night that they were released (Table 5). Of these several were watched swimming slowly head-first downstream along the beck bottom.

The other twenty-six eels must have gone to ground or, more likely, swum back upstream into the lake. Of the fourteen eels retrapped eleven out of twenty were recaught on a night when there was a slight natural run (seven eels in 3 hr.), whereas on the

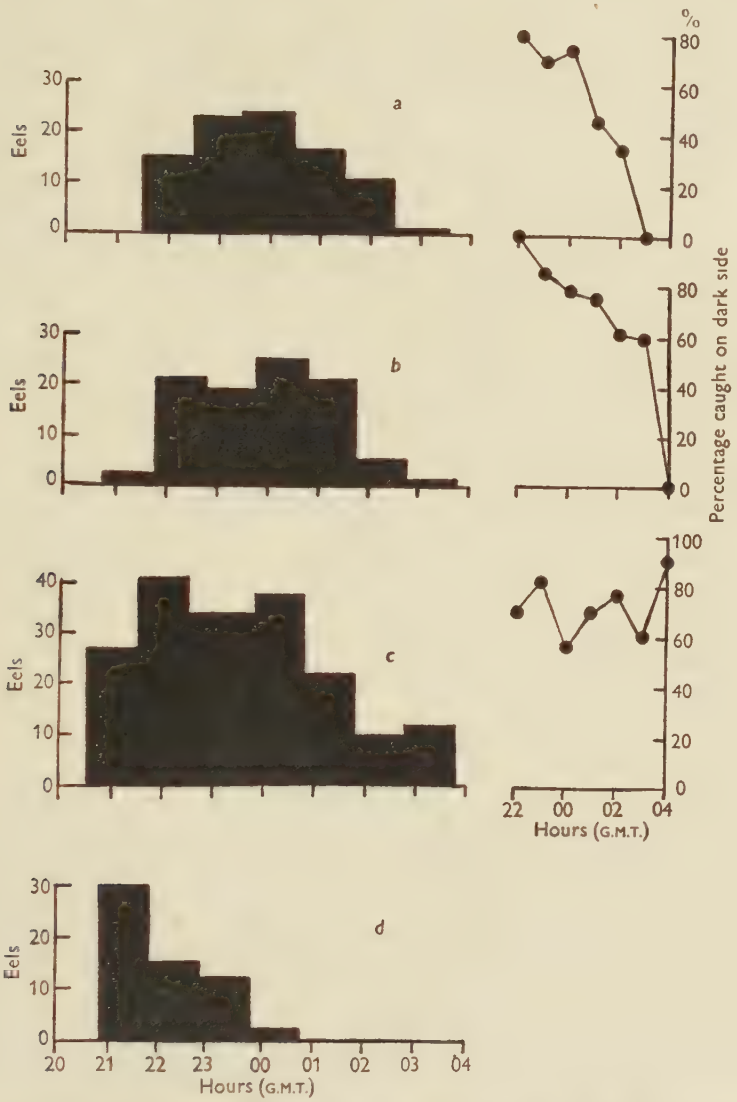

Fig. 5. Hourly catches of eels in the Cunsey Beck trap during 4 nights in 1943. The percentage of the eels caught which entered the dark side of the trap is also shown. (*a*) 8–9 Aug.; water-level 14·5–15·5 in.; 88 eels. (*b*) 28–29 Aug.; water-level 13·5–14·5 in.; 89 eels. (*c*) 29–30 Aug.; water-level 19·5–24·5 in.; 185 eels. (*d*) 30–31 Aug.; water-level 26–24 in.; 53 eels.

other occasion there was no natural run and only three out of twenty eels moved downstream into the traps.

Only five of the marked eels returned to Esthwaite Water were retrapped, although the Cunsey Beck traps were fished day and night throughout the season (Table 6). The marks on these five eels and the eels themselves were in good condition when

retrapped. No eels returned under 20 days; this may be explained by the absence of conditions leading to a large-scale migration during this period, though none of the four returns from the outflow end of the lake were recaught on the first night of the next big flood. The eel from the north end of Esthwaite took 58 days to cover the 2½ miles.

Table 5. *Eels recaptured during attempts to induce runs of silver eels in Cunsey Beck in* 1942

	Range of water-level (in.)	Conditions	Natural run	No. liberated	No. recovered and time
15 Aug.	15–15	Fine, starlight	7 eels in 3 hr.	10	6 in 35 min. 2 in 45 min.
				10	3 in 20 min.
21 Aug.	10–10	No rain, light overcast, no wind	0 eel in 1 hr.	10	1 in 30 min.
				10	1 in 30 min. 1 in 40 min.
Total				40	14

Table 6. *Recapture of marked eels returned to Esthwaite 9 August* 1943

Eels originally caught in the Cunsey trap 8–9 August.

Esthwaite station at which released	No. of eels released	Date of recapture	No. recaught	No. of days in lake	No. of eels not returned
South end, approx. 520 yd. from Cunsey Beck	18	28–29 Aug.	1	20	—
		29–30 Aug.	1	20–21	—
		31 Aug.–1 Sept.	1	23	—
		1–2 Sept.	1	24	14
Middle of lake ⅛ of a mile from Cunsey Beck	20	No return	0	—	20
North end, 1½ miles from Cunsey Beck	19	5–6 Oct.	1	58	18

LIGHT EXPERIMENTS IN THE FIELD

(*a*) *Methods*

Most of the field experiments on the responses of migrating silver eels to light were made on Cunsey Beck, as this was the only site where the whole width of the stream was fished so that all the eels swimming through the light barrier were caught, giving complete experimental control. At Nibthwaite, Dalemain and Corby Castle it was impossible to fish the whole width of the river. At these three sites underwater lights were placed at an angle to the current to see whether the eels would be deflected away from a weir into a trap at the side of the stream. The effect of the lights was then tested by fishing the traps with lights on and off for alternate periods and applying the normal approximation to the binomial test to the difference in numbers of eels caught with and without the use of lights. In using this test it was assumed that runs during lights-on and lights-off periods were equal during the night as a whole, and that the number of eels open to capture formed a very small proportion of those running on the particular night concerned.

The underwater electric lighting used in the field experiments had to be designed to emit as little light as possible to the air owing to war-time 'blackout' restrictions. The lights were mounted in metal tubes 3 ft. long slung by special hooks at 2 ft. 6 in. to 3 ft. intervals from two wires spanning the stream; these hooks allowed the lights to

swing in the direction of the current only (Fig. 6) so as to let tree trunks and rubbish pass below the lights without impediment and without damaging the rigging. Electric current was provided by 12 or 6 V accumulators. To restrict and direct the light beam two types of cap were used. In early experiments a metal cap directed the beam of light more or less vertically downward (Fig. 6*a*), depending on the speed of the current, and the beam from each light overlapped those of its two neighbours to give a strip of light along the bottom of the stream varying from 1 to 3 ft. wide with increasing depth of water. In flood conditions the lights swung out too far to give the desired effect, throwing the light downstream. The metal caps were therefore replaced by celluloid caps which directed the light upstream (Fig. 6*b*) so as to be seen by the down-coming eels as a series of bright blobs rather than a continuous wall of light. Algae and *Simulium* larvae and pupae attached themselves to the outside of the caps and made it

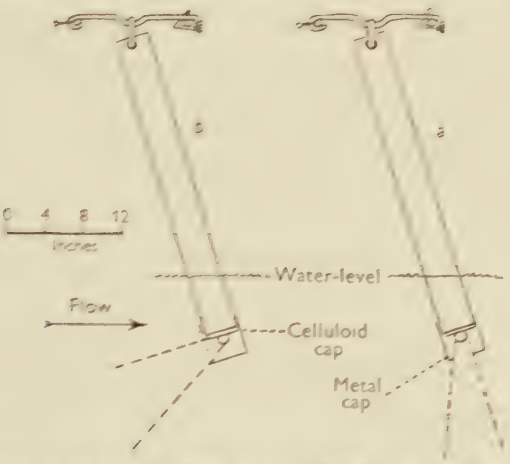

Fig. 6. The lamp housings seen in side view as suspended from two aerial wires stretched across the river (*a*) fitted with the earlier metal cap, (*b*) with the celluloid cap used later.

necessary to remove and clean them regularly. The 6 V bulbs used at Nibthwaite and Dalemain were 0·3 A, each light giving about 3 c.p., and the 12 V bulbs used at Cunsey Beck and Corby Castle were 3 or 4 W, each giving about 5 c.p. Other apparatus and methods are described site by site in association with particular experiments.

(b) Light as a barrier to migrating silver eels

Observations on the effect of light in stopping the run were the outcome of experiments on the Cunsey Beck in 1944 when an unsuccessful attempt was made to guide eels by light into a Coghill net at the side of the beck (Fig. 7). A line of underwater lights was fixed across the beck just below the outflow of Esthwaite Water and about 80 yd. above the two eel traps which provided a control by catching any eels passing through the light path. The light line consisted of twenty-three 12 V lights 2 ft. 6 in. apart and at an angle of 37° to the current, stretched from the left bank to the outer pole of the 8 ft. wide net. Two light intensities were tried, each light giving about 5·3 or 0·25 c.p. The water speed at the surface below the lights was found to be 2·3 ft. sec. (when the water level recorded 10 in.). Lights were switched on or off for alternating half-hourly periods: after each half-hour the net was examined for eels,

and after 1 min., to allow any eels between the nets and traps to 'clear', the traps were changed. Had the lights been effective in deflecting the eels into the Coghill net, the ratio of the number of eels in the net to the number in the traps when the lights were on and for control periods in the dark would have expressed the effect of the lights.

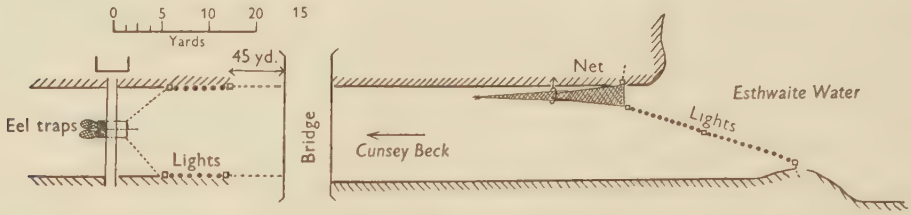

Fig. 7. Cunsey Beck site, 1944. Plan showing the arrangement of the Coghill net and light barrier.

Only three eels were caught in the Coghill net, but a comparison of the number of eels in the traps when the lights were on and for control periods without lights showed that the lights were effective in stopping the run. These results are summarized in Table 7. With the brighter lights (5·3 c.p.) nine eels were trapped with the lights on and ninety-five in control periods in the dark, whereas with the dimmer lights (0·25 c.p.) ten eels were trapped with the lights on and thirty-eight in the dark, also a statistically highly significant result. The brighter lights here seemed to form a slightly more effective barrier. Throughout these experiments the intervals of light and darkness were half an hour in length.

Table 7. *Results of experiments on the Cunsey Beck using the Coghill net in* 1944

		Water-level		Lights on			Lights off			% in trap with light off	Significance (*P*)
	Candle-power	Start (in.)	Finish (in.)	No. of times	No. of eels Net	Traps	No. of times	No. of eels Net	Traps		
28–29 Aug.	5·3	11	11	8	1	9	8	1	95	91	$6{\cdot}2\times10^{-16}$**
7–8 Sept.	0·25	16½	16½	3	1	2	3	0	8	—	—
15–16 Sept.	0·25	5¼	7	8	0	8	8	0	30	—	—
Total 0·25 c.p.	0·25			11	1	10	11	0	38	79	$9{\cdot}6\times10^{-5}$**

(*c*) *The deflexion of migrating silver eels by light*

The arrangements of lighting systems in relation to eel traps at the four sites at which field experiments were carried out on the reactions of migrating eels to light are shown in Figs. 8–11. Most of these light experiments were made at the Cunsey Beck site. The stream was divided by a median partition, and the traps, leads and lighting systems were arranged so that each side of the beck was a mirror image of the other (Fig. 8). This plan was the same in all four years, 1941–4. In 1942 a single light barrier was used on each side of the beck, consisting of eleven 12 V, 4 W lights at 2 ft. 6 in. intervals slung at 24° to the current, capped to form a continuous light path in early experiments and later to throw the light upstream. In 1943 two lighting systems, throwing the light upstream, were used, one of six lights at 3 ft. intervals at 35° to the current, and another of fifteen lights at 2 ft. 6 in. to 3 ft. intervals at 12° to the current. In all the experiments the lights on each side of the stream were lit for

alternating quarter, half or hourly periods and at the end of each period the lit side of the stream was changed and eels from both or all the traps were counted.

Lighting experiments* at the other three sites were confined to 1942. At all three a

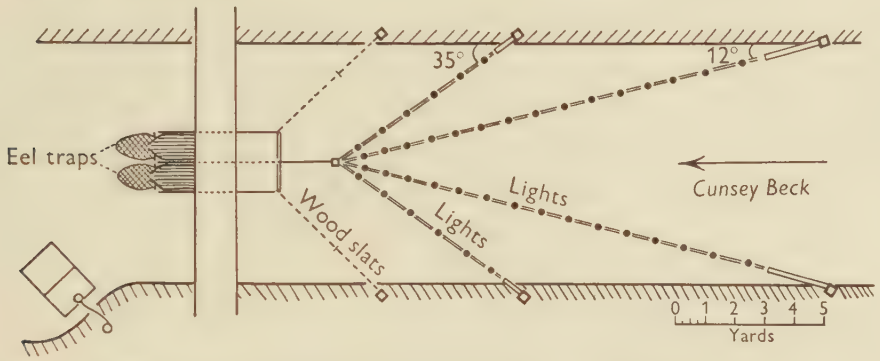

Fig. 8. Cunsey Beck site, 1943. Arrangement of lights and traps.

line of lights was fixed, at an angle to the current, leading to an eel trap at the side of the stream. Lights were switched on and off for alternating hourly or half-hourly periods, and the number of eels trapped during each period was counted. The effect of the lights was estimated by the difference in catches with and without the lights. At Nibthwaite (Fig. 9) the eel trap was in a cut from a mill leat back to the main river. The main current was along the right bank of the river opposite the entrance to the mill leat, and the river continued over a rough boulder weir. To enter the mill leat the eels had to be deflected round a prominent mud bank. The amounts of water

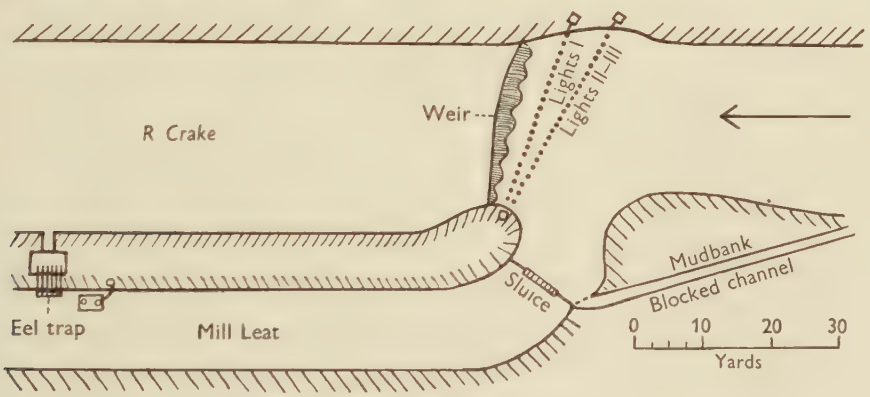

Fig. 9. Plan of the Nibthwaite site.

flowing into the leat and through the trap were controlled by sluices. The trap was 72 yd. down the leat from the river so there was a possibility of error arising from the time taken for the eels to swim down the leat. A light barrier of twenty (later twenty-four) 6 V, 0·3 A lights was slung slightly upstream of the weir in an attempt to deflect the eels into the leat round the prominent mud bank. A continuous light path and upstream-shining lights were tried.

* Miss J. Storey was in charge of experiments at Nibthwaite, Mr E. D. LeCren at Dalemain, and Mr J. W. L. Beament and Mr P. Tuft at Corby Castle.

At Dalemain (Fig. 10) sixty-two 6 V lights at 3 ft. intervals were fixed along the upstream side of the 60 yd. weir, which was built at a very acute angle to the current, and had a 2 ft. vertical concrete face for directing water through the eel trap. It

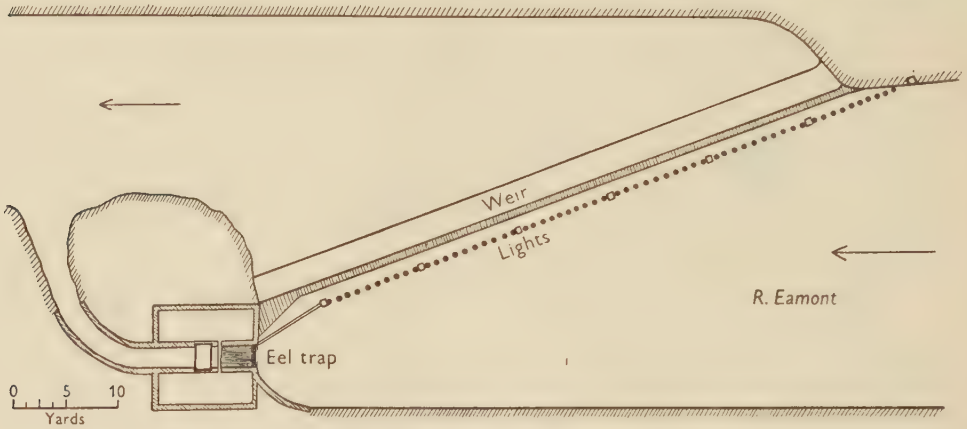

Fig. 10. Plan of the Dalemain site.

became clear during the experiments that except during high floods (when up to 20 in. of water might flow over the weir) this trap probably caught almost all the eels without the use of lights. Consequently the lights only came into effect on the very few nights of high floods.

The River Eden at Corby Castle is divided into two parts by an island (Fig. 11) and the part near the right bank flows through four gaps between stone piers, a weir along-

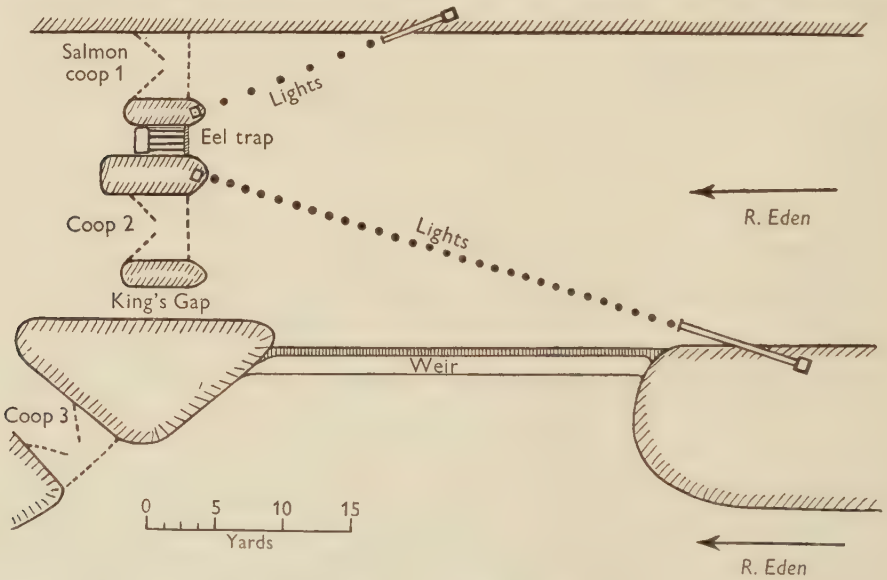

Fig. 11. Plan of the Corby Castle site.

side taking flood water. The eel trap was in one of these two gaps, the wider gaps were occupied by salmon coops and the one nearest the weir was a permanent King's gap. Two light barriers led to the trap (Fig. 11). The long arm of twenty-eight 12 V lights

at 3 ft. intervals was designed to head off the eels from the main current of water through the King's gap and over the weir. The shorter arm of six 12 V lights was little used as the salmon coop below it was blocked for repairs. There was no lake to buffer the effect of the rain so the river rose rapidly at this site and only on very few nights were conditions practicable for light experiments. This site was chosen partly to see if lights would prove effective in deflecting migrating eels in a river which was not near any lake outflow and where the eels would be well under way, and whether the lights would affect the eels in a river which becomes muddy in flood and without the aid of any physical barrier, and partly to demonstrate that eel trapping need not interfere with salmon fisheries.

Table 8. *Results of lighting experiments on the Cunsey Beck*, 1941–4

		No. of nights	Range of water-level (in.)	No. of eels			% trapped dark side	Significance (*P*)
				Total	Lit side	Dark side		
1941	(one series)	2	13·5–27	15	3	12	80	0·035*
1942	Series I, metal caps†	9	8–15	74	25	49	66	0·0075**
	Series II, no caps	3	20·5–27·5	138	74	64	46	0·45
	Series III, celluloid caps†	3	11–29·5	17	3	14	82	0·0127*
	Total (3 series)	17	8–29·5	229	102	127	55	0·112
1943	Series I, double light barrier§	6½	7·5–26	157	49	108	69	$1·7 \times 10^{-6}$**
	Series II, short line only§	4	11–24·5	290	77	213	73	$1·3 \times 10^{-12}$**
	Series III, long line only§	1½	23·5–26	29	9	20	69	0·0629
	Total (3 series)	12	7·5–26	476	135	341	72	$1·1 \times 10^{-19}$**
1944	Dim lights along bank‡	1	6–9	42	17	25	60	0·280
1942	8 Aug., metal caps	1	11–12	22	4	18	82	0·0056**
	5 Sept., no caps	1	27·5–27	123	65	58	47	0·589
1943	8 Aug., double barrier	1	14·5–15	97	35	62	64	0·0083**
	28 Aug., short line only	1	13·5–14	94	23	71	75	$1·2 \times 10^{-6}$**
	29 Aug., short line only	1	19·5–24	185	51	134	72	$9·9 \times 10^{-10}$**
	30 Aug., double barrier	½	26–24	26	4	22	85	$8·7 \times 10^{-4}$**
	30 Aug., long line only	½		23	8	15	65	0·2113

† See Fig. 6. § See Fig. 8. ‡ See Fig. 7.

The most definite results came from Cunsey Beck in 1942 and 1943 (Table 8). Although the differences were not always significant the numbers of eels trapped on the dark side of the beck were consistently higher than on the lit side throughout all the experiments except for a few nights during the high floods of 1942. In 1942 the continuous light path had a considerable effect. Catches of eels were small when the upstream-shining lights were used, but the results indicated that the eels responded more markedly to such lights. In 1943 the lights were directed upstream and there was an excellent run of eels; the effect of light on the migrating eels was tried on twelve nights and 72% of the 476 eels trapped were caught on the dark side of the stream. The normal approximation to the binomial test shows this difference to be highly significant. Except when the long line of lights was used alone (Fig. 8) lights made a highly significant difference to the catches on each of the four nights when more than thirty eels were caught. During two of the three nights in 1943 when more than eighty eels were caught the percentage of eels taken on the dark side of the beck decreased steadily as the night progressed (Table 9 and Fig. 5). This was not due to

the lights becoming dimmer, since new batteries were used halfway through one night, nor to the current speed becoming faster, for on the night of the most strongly rising flood this fall off did not occur (Fig. 5*c*). Twenty-seven small yellow eels ('snigs') were caught in ones and twos throughout the 1943 season in the Cunsey Beck eel traps. Twenty-five (92%) were from traps on the dark side of the beck, whereas only 72% of the 476 silver eels were trapped on the dark side.

Table 9. *The number of eels trapped on the dark side of the Cunsey Beck during each of the three nights in* 1943 *when over eighty eels were taken during one lighting experiment*

	Range of water-level (in.)	Times at which lighting experiments started (G.M.T.)		Hours of lighting experiments 1	2	3	4	5	6	7	Total
8–9 Aug.	14·5–15·5	2125	Total no.	15	22	22	18	9	2	—	88
			No. on dark side	12	16	16	9	2	(1)	—	55+(1)
			% on dark side	80	73	73	50	22	(50)	—	62·5
28–29 Aug.	13·5–14·5	2040	Total no.	2	17	13	26	19	9	2	88
			No. on dark side	2	14	12	20	11	5	2	66
			% on dark side	100	82	92	77	58	56	100	75
29–30 Aug.	19·5–24·5	2036	Total no.	27	38	34	38	20	12	10	179
			No. on dark side	19	31	18	27	16	8	9	128
			% on dark side	70	82	53	71	80	67	90	71·5

Table 10. *Results of lighting experiments at Nibthwaite in* 1942

	Date	No. of nights	Range of water-level (in.)	Total eels	Lights off Hr.	Lights off Eels	Lights on Hr.	Lights on Eels	% caught with lights on	Significance (*P*)
Series I, 20 lights with metal caps	8–11 Aug.	4	10·3–13·5	15	5½	8	4	7	47	—
Series II, 24 lights, 20 with metal caps	1–9 Sept.	8	8·5–20	311	20	151	20	160	51	0·653
Series III, 24 lights with celluloid caps	1–12 Oct.	5	10–19	177	14	54	15	123	70	$3{\cdot}2\times10^{-7}$**
Total	—	17	8·5–20	503	39½	213	39	290	(58)	$7{\cdot}0\times10^{-4}$**
Series II	5 Sept.	1	9–20	179	3	90	3	89	50	—
				199	4	105	4	94	47	0·478
Series II	6 Sept.	1	20–19	52	2	21	2	31	60	0·211
				64	3	27	3	37	58	0·263
Series III	9 Oct.	1	12–19	133	5	29	5	104	78	$9{\cdot}9\times10^{-10}$**
				78	4	29	4	49	59	0·033*
Series III, 'low' flood	8–9 Oct.	2	10–19	135	7	29	7	106	78	$9{\cdot}9\times10^{-10}$**
Series III, 'high' flood	10–12 Oct.	3	19–20	42	8	25	8	17	40	0·280

Notes (i) The first section of the table includes all the season's observations. In series II and III the angle of the light beams was more acute than in Series I.

(ii) The second section gives the results of single nights. The catches during 'lights on' periods are compared first (upper figures) with the succeeding 'lights off' periods, and then (lower figures) with the preceding periods, in order to minimize the effects of fluctuations in the numbers of eels migrating. In this section the water-level figures refer to the beginning and end respectively of the observation period.

(iii) In the third section two groups of nights are compared to show the effect of river conditions.

Results from experiments at Nibthwaite supported those obtained from Cunsey Beck. It is clear from Table 10 that the total catch was higher when the lights were on than for control periods without the lights, showing that the lights had deflected the eels into the mill leat. Analysis of the season's total into the component series of experiments shows that here, as at Cunsey Beck, the upstream-directed lights had the most effect; with these lights 70% of the 177 eels were taken when the lights were

on, a highly significant result ($P = 3{\cdot}2 \times 10^{-7}$), whereas with downward-directed lights (series II) the lights had no significant effect. Data using upstream-directed lights are shown separately for 'low' and 'high' (over 19 in. of water) floods, and it will be seen that this effect of the light was only significant in low flood when the water was flowing less swiftly.

At Dalemain (Table 11) the results were complicated by the irregularity of the natural run, or by the lights checking the run instead of deflecting the eels. This rendered control of the experiment by having alternate periods with and without lights untrustworthy. For example, during a dark period in the second lot of experiments, 150 eels arrived in 10 min. Up till the night of this very irregular run, in nine experiments using downwardly-directed light 56% of the 374 eels were trapped when the lights were on, but as periods with lights on totalled 1½ hr. longer than the control periods the number of eels trapped per hour, 19·2 and 16·5 respectively, was not very different. Except on the night of the irregular run, when 99% of the catch arrived

Table 11. *Results of lighting experiments at Dalemain,* 1942 *and* 1944

		Date	No. of nights	Range of water-level (in.)	Total eels	Lights off		Lights on		% caught with lights on	Significance (P)
						Hr.	Eels	Hr.	Eels		
1942	Series I, metal caps	2 Aug.–4 Sept.	9	3·2–18	374	10	165	11½	209	56	0·026*
	Series I, metal caps	5–9 Sept.	4	12–21	182	3½	176	3	6	(3)	—
	Series II, celluloid caps	23 Sept.–13 Oct.	2	9·5–14	18	2	7	1½	11	61	0·481
1944	Series I, metal caps	1 Sept.	1	3·2–2·7	55	1	22	1½	33	60	0·177
		2 Sept.	1	2·7–5·2	35	1	15	1	20	57	0·496
		3 Sept.	1	5·2–4·5	131	1½	66	1	65	50	—
		4 Sept.	1	4·5–21	97	1½	43	1½	54	60	0·312
		5 Sept.	1	21–18·5	174	1½	172	1½	2	(1)	—

during one dark period, differences between catches with and without lights were not significant for any single night. Too few eels were trapped after the upstream-shining lights were fitted to give a definite result. Thus at Dalemain the lights appeared to have a deflecting effect during the first period, after which no conclusion as to the effect of the lights could be reached.

At Corby Castle 1942 was an unfortunate season as an exceptionally high flood came up suddenly bringing with it a large tree which damaged the apparatus. Therefore few lighting experiments were done and too few eels taken for the results to be significant. Results tended, however, to support conclusions reached at Cunsey Beck and Nibthwaite, for of the thirty-seven eels trapped during seven nights, twenty-seven were taken when the lights were on and ten during control periods.

LABORATORY EXPERIMENTS

(*a*) *The artificial river and the reactions of silver eels to water flow*

Experiments made by Miss M. E. Brown at Wray Castle in 1941, using tanks of still water, showed that dark-adapted eels reacted to light presented in various ways. As the behaviour in still water was so difficult to compare with behaviour in a current, a special artificial river was built in the cellar at Wray Castle. This artificial river (Fig. 12) consisted of an oblong concrete tank divided into two channels by an oblong partition round which water was driven in a continuous stream. The two straight channels were 15 ft. long, one 2 ft. the other 3 ft. wide. The whole tank contained water up to 15 in. deep, driven round at a constant speed by a propeller belt-driven

by a $\frac{1}{8}$ h.p. electric motor. Speeds of flow from about 0·5 to 2 ft./sec. were possible by altering the pulley ratio. The propeller channel was sunken so that water could be circulated when only a few inches deep in the tank, and was made inaccessible to the eels by two wire screens at *X* and *Y*. A hole *E* enabled eels to pass from *Y* to *X* and so to continue swimming round the tank. Guide vanes were fitted in the bends to reduce eddy formation. The whole apparatus was tar-varnished black and was in a dark room with dull black walls. The eels were caught in the Cunsey Beck traps in autumn and were stored in the dark. Most of the silver eels migrating from Esthwaite were females about 50–65 cm. long (see Frost 1945), so the silver eels used throughout the laboratory experiments were all females and of comparable sizes. All the eels were dark-adapted for at least three-quarters of an hour before each experimental trial.

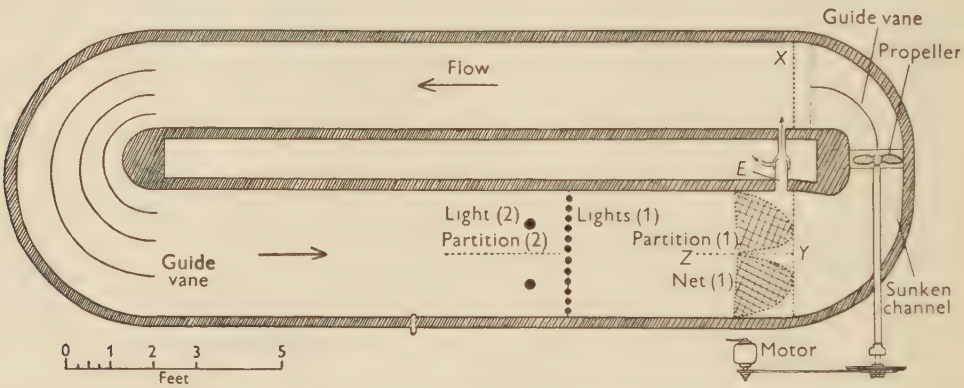

Fig. 12. The 'artificial river' used in laboratory experiments. The lights and trapping system labelled (1) were used in experiments on the effect of light as a barrier to eels swimming downstream. The lights and partition labelled (2) were used in experiments giving the choice between a dark or a light channel. In the latter experiments the eels were guided through passage *E* and continued to swim round the tank.

The reaction of the eel to the current has to be kept in mind when considering the light experiments in the artificial river. The silver eels tended to swim upstream against the current unless they were brought back from the Cunsey Beck traps and 'run' in the artificial river the same night, though after the eels had been kept in tanks in the laboratory for several months they tended to swim head-first downstream more often. Throughout the experiments there was considerable variation in reaction from eel to eel. In a dim diffuse light the eels, possibly because of the light, swam upstream against the current. Tests were made with these eels to find what speeds of flow a silver eel can swim against and how long it can maintain its position against such speeds. These trials were made at the following water speeds:

	Surface flow (ft./sec.)	Bottom flow (ft./sec.)	Average speed (ft./sec.)
'Slow'	0·96	0·73	0·83
'Medium'	1·21	1·09	1·15
'Fast'	1·71	1·71	1·71

It was found that the faster the current the more these upstream-swimming eels struggled against it. These eels could make good headway against a flow of 1·1 ft./sec., but against a 1·7 ft./sec. flow they could swim for short bursts only and tired rapidly.

On three occasions eels were brought from the eel trap on Cunsey Beck and 'run' in the artificial river the same night. On the first occasion, 17 August 1943, when eleven eels were brought from a rising flood at Cunsey Beck, they swam actively head-first downstream in the laboratory. On the second and third occasions, 11 and 18 September 1943, six and two eels respectively were taken after several days of flood when many eels had already been trapped the previous day or two; these eels were not nearly so active, and soon turned and swam upstream into the current.

Two types of lighting experiments were made in the artificial river. First, the effect of a wall of light across the channel in delaying the downstream swim of the eels was tried. Secondly, downstream-swimming eels were run one at a time and presented with the choice of a dark or a lit passage.

(*b*) *Light as a barrier to silver eels*

A wall of light was thrown across the channel (Fig. 12), at right angles to the current, by twelve 12 V, 10 W bulbs 2½ in. apart fixed just below the water-level. Two intensities regulated by a rheostat were used giving 5·6 and 0·006 c.p. per bulb. These trials were made in January 1943, the sixty eels used being kept as described above.

Table 12. *Results of experiments in the artificial river on the effect of light as a barrier to the passage of eels*

(The 'bright' lights each gave 5·6 c.p.; the 'dim' ones 0·006 c.p.)

	FIRST TRIAL No. of eels trapped in each 5 min. period				SECOND TRIAL No. of eels trapped in each 5 min. period			
Min.	Dark	Dim	Dark	Bright	Dark	Dim	Dark	Bright
	Water speed, 1·1 ft./sec.				Water speed, 1·1 ft./sec.			
0–5	30	16	33	17	31	19	31	15
5–10	16	17	13	22	12	15	13	15
10–15	2	7	6	5	3	5	4	7
15–20	3	4	4	4	6	3	3	5
20–25	7	2	1	4	1	5	3	8
25–30	0	3	3	2	3	1	4	2
>30	2	11	0	6	4	12	2	8
	Water speed, 0·8 ft./sec.				Water speed, 1·7 ft./sec.			
0–5	12	7	10	8	39	29	38	31
5–10	13	11	19	10	10	16	14	16
10–15	14	6	6	7	4	4	3	4
15–20	8	8	10	5	3	1	4	2
20–25	4	7	5	3	1	4	1	2
25–30	2	4	4	7	0	1	0	3
>30	7	17	6	20	3	5	0	2

The dark-adapted eels were poured ten at a time into the circulating river at *X*, and any eels in the nets at *Y* were removed after 5, 10, 15, 20, 25 and 30 min. Six 'runs' of ten eels were made at each water speed, and control runs were made in total darkness. As the same sixty eels were used throughout these trials, some eels were tried first with lights on and others were tested first in total darkness to counteract any effect the previous experience of the eel might have on its subsequent behaviour. Runs in the medium speed of current were repeated at the end of the experiment to provide a check as to the effect of frequent trials on the eels. The major difficulty was to trap the eels

so that they could not return upstream again and yet to offer no resistance to other down-coming eels, and the method used throughout this experiment was to drop a wire screen at *Z* after each 5 min. period and empty the two nets as quickly as possible. It was noticed, however, that eels occasionally swam back upstream through the lights and so were not recorded until a later period. This might happen after the eel had almost or completely entered the nets, either immediately or after a minute or two. Tests showed that this also happened in total darkness, and it was probably, at least in part, a current response. The light could not be shielded from the nets and it seemed that the eels swam back upstream again more often when the lights were on, although this was not proved. If this was so, then the effect of the light shown here was

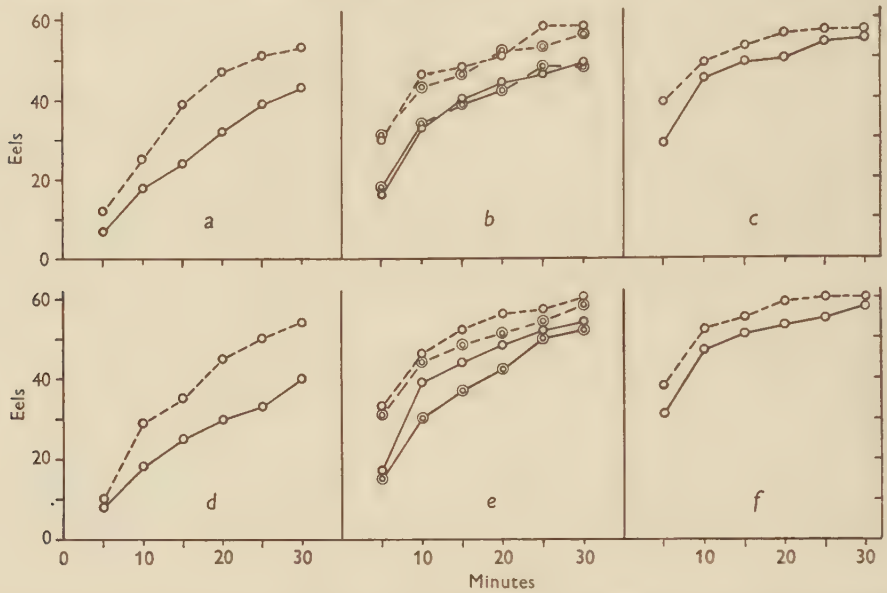

Fig. 13. Light as a barrier to eels swimming downstream in the artificial river. Each curve shows the total number of eels in six runs, ten eels being used for each run, plotted cumulatively against the time at which the eels were trapped. Runs were made at two light intensities: *a–c* at 0·075 c.p., *d–f* at 67·95 c.p. Three current speeds were used: 0·8 ft./sec. in *a* and *d*, 1·1 ft./sec. in *b* and *e*, 1·7 ft./sec. in *c* and *f*. Pecked curves—control runs in total darkness; full-line curves—runs with light barrier in use; ◎—repeat trials at 1·1 ft./sec.

probably not due solely to a negatively phototatic response, but to a combination of this and a photokinetic response, the eels being activated by the light to swim in the only possible direction, upstream again, more frequently than they did in the dark. Results are summarized in Table 12 and Fig. 13. In Fig. 13 the numbers of eels trapped in each 5 min. period are plotted as cumulative totals, trials at different current speeds and with different light intensities being plotted separately, and each curve is for sixty eels. The difference between the complete and dotted lines represents the effect of the light on the behaviour of the eels. Although this difference is not great it is consistent, as at all three speeds and with both light intensities the trapping of the eels was delayed when the light was on.

(c) *Choice between dark or lit channels*

The eels were presented with the choice of a dark or lit passage in the 3 ft. wide channel of the artificial river (Fig. 12). One 12 V, 6 W bulb was fixed each side of a light-proof partition which divided part of this channel into two passages. Each light was just below the water surface and capped to throw the light upstream. The two passages were lighted alternatively. To avoid any complication of results by eels swimming back upstream the eels were used singly. Only eels travelling headfirst downstream were used, and these were allowed to pass through the tube *E* and to continue swimming round the tank, the lit side being changed each time. The eels were recorded each time they passed through the lit or dark passage, until they had reached a maximum of thirty 'runs' or until they started to swim upstream. If an eel had not appeared downstream after 3 min. it was removed from the tank. This experiment was conducted at two current speeds, averaging 1·15 and 1·71 ft./sec., and at both speeds two light intensities giving 21·4 and 4·0 c.p., were tried. The effect of a strip light, giving 9·0 c.p. was also tried.

Table 13. *Results of experiments on the choice between a dark or a lit passage in the artificial river*

Lighting (c.p.)	Speed (f./sec.)	Total no. of trials*	Total no. of 'runs'*	No. of eels passing: Dark passage	No. of eels passing: Lit passage	% of total down dark side	Significance (*P*)
4·0	1·1	70	322	194	128	60	$2{\cdot}9 \times 10^{-4(**)}$
4·0	1·7	29	82	43	39	52	0·741
21·4	1·1	8	27	14	13	52	—
21·4	1·7	20	104	55	49	53	0·624
9·0 (strip light)	1·1	39	60	35	25	58	0·246

* A 'trial' represents the use of one eel; the 'runs' represent the number of times an eel encircled the tank.

The results are given in Table 13 which shows that only the first of these trials gave a significant result. These experiments were not continued as it was felt that the eels were influenced too much by the abnormal conditions in the tank for results to be applied to natural conditions.

DISCUSSION

(a) *Factors influencing the seaward migration*

The numbers of eels migrating on any night will depend on three things: the number of silver eels available in the lake or river, the external conditions, and the responsiveness of the eels to these external conditions. As so many eels run on so few nights and the activity and number of eels migrating are greater in high floods and on dark nights, it seems that the external conditions are very important in determining the number of the available silver eels that will migrate on any night. It follows from this that the 'migration mood' must be produced in eels which are in various stages of physiological preparedness for migration; a deduction which is supported by the catches during high floods including eels migrating actively although not yet fully silver. It follows also that the stimulus initiating the migration must be some factor, or combination of

factors, which can vary in degree, since the degree of response is proportional to the strength of the stimulus and it is not an 'all or none' reaction in which the response would only occur once the stimulus crossed a fixed threshold value. There will be no fixed threshold value of the external stimulus which starts the migration as this will depend on the responsiveness of the eel.

Silver eels migrated only during the autumn months. It is of interest that Cairns (1943) found the same for two species of New Zealand eels, *Anguilla dieffenbachii* Gray and *A. australis schmidtii* Phillips. The migration of european silver eels is most affected by floods and the phase of the moon. In certain rivers, as in Cunsey Beck and, it is reported, in rivers in Cyprus, after summer droughts it would only be possible for the eels to migrate down the river after a flood. Reports from Blagdon reservoir state that large numbers of eels migrate from this reservoir in early spring, the only time that the water-level allows them to do so. Jacobson & Johansen (1922) mention that in the small brooks in Denmark eels are delayed from migrating in dry summers, and at least some of them migrate to sea in the following spring. In deeper rivers, too, such as the River Leven and the River Bann, eels evidently do not begin to migrate until there is a flood. On the Bann the legal eel fishing season starts in June, but eels are not caught until there is a good flood, which delayed the catch of the first eels until August in 1933 and 1935 (Frost, unpublished data). Thus there is strong evidence that the initial stimulus to migration comes from flood or some associated factor. Floods may affect the eel in several ways, mechanically or by changes in temperature or other physical or chemical changes. Some silver eels kept in a sink below a window in a damp, unheated, tankroom tended to leap out of this sink and other tanks more often on dark nights after a fall in temperature of about 1° C., and generally on the same nights that eels were migrating in the field. Though the data are very incomplete, this does suggest that the temperature drop associated with autumn floods may be an important factor in initiating migration, as here there was no possibility of a rise in water-level affecting the eels. Bull (1936) has shown the perception of minute temperature changes by fish, e.g. 0·03–0·05° C. by *Blennius pholos* L. During the autumn the water temperature is likely to be falling almost continuously and this may help to explain the migration of eels on dark nights when there is no flood. Frost (1950) reports, however, that eel fishermen on the River Bann say that eels do not run on frosty nights, though whether this is a temperature effect or due to associated clear skies and bright starlight is not known. It is also said that eels do not run on misty nights. Here again, the diffusion of any light by a mist, or the difference between air and water temperature, may affect the eels. Salmon are said to be affected by differences between air and water temperatures, 'rising' when the river temperature is lower than the air temperature (Taverner 1931, p. 232.)

The increased catches of eels when the rivers are in flood suggest that flood may be a guiding factor leading the already active eels to the outflow of a lake, as for example in early October 1942 at Newby Bridge (Fig. 2). The flood may also aid the migration mechanically as the eels once in a fast stretch of river in complete darkness may be unable to orientate in the absence of eddies (see Gray 1937 and below). In this case the eels would be swept down towards the sea, and the flood would be hastening migration in the same way as Pritchard (1944) concluded it did for fry of the pink

salmon *Oncorhynchus gorbuscha* (Walbaum). Eels are very sensitive to vibrations in the water, as Wunder (1927) has shown. Floods might also affect the eels through one of many possible coincident physical or chemical factors but more knowledge of these is necessary before the rôle of these can be considered. The culminating peak run, occurring if a flood terminates a dark period of the moon during which eels have been migrating, as in September 1942 at Dalemain and in October 1942 at Newby Bridge (Fig. 2) provides some measure of the effect of the flood. Fig. 2 shows clearly that some eels migrated before the flood, but that a great many more were evidently available and ran as soon as there was a flood. The flood may have acted as a trigger to eels not quite as physiologically prepared as those eels migrating when there was no flood, or an increased number of active eels may have been guided to the lake outflow on the same night by the directional pull of the current.

The phase of the moon probably influences the eel migration through the effect of the light rather than any unexplained periodic effect, since under certain circumstances eels will run at full moon, e.g. at Dalemain in August 1943 (when part of the river was very turbid). The Cunsey Beck traps, and often the Dalemain traps, were fished day and night but never once was a silver eel caught by day. There is, moreover, evidence both that light inhibits the migration and that darkness or some associated factor may encourage it. The inhibiting effect of light is indicated by the stopping of the runs by day and the almost complete cessation of eel runs over full moon periods, even with a rising flood as at Cunsey Beck in early September 1944 (Fig. 4). Many times there was a good run of eels on the dark of the moon even though there was no flood, e.g. at Dalemain in September 1942 (Fig. 2), which suggests either that darkness or some associated factor initiated the migration or else that eels do not need an external trigger stimulus each night provided that light does not inhibit their movement (see below). If the effect of the moon in delaying the run is only due to light, then the weather conditions, particularly the amount of cloud, will modify the effect of the moon; this is stated to be the case by fishermen on the River Bann in Northern Ireland (Frost 1950). Light is known to affect the pituitary secretions of many animals and histological evidence suggests that these secretions are probably closely connected with migration in the eel (Evans 1940).

The effect of light in stopping the run has been demonstrated at Cunsey Beck where a line of lights across the beck source, each light giving about 0·25 c.p., was effective in preventing the eel run for half-hour periods, the longest periods tried. Laboratory experiments indicated that not only does light stop the run of eels, but that non-migrating silver eels, contrary to migrating eels, tend to move about more when in the light and so tend to accumulate in dark places. This was suggested by early experiments in still-water tanks in the laboratory where the shock effect of light appeared important in eliciting the negative phototactic response in silver eels. Once the initial shock effect had worn off the eels responded to the light photokinetically. Eels in a still-water tank with one half in darkness and the other illuminated by a dim overhead light tended to move about more in the lit half, and this photokinetic response led them to accumulate in the dark half of the tank where they remained inactive. Experiments in the artificial river supported the idea that once the shock effect of the light has worn off the light may activate the eel to respond in a non-directional manner.

This helps to explain what happens to the silver eels by day. Daylight will check the run and the photokinetic response will lead the eels to hide away by day in some dark place, where they probably remain until nightfall.

It appears therefore that some external stimulus, associated with flood, acts as a trigger to downstream movement, though it is not yet clear how this operates and how long the effect of its stimulation will last. The alternatives are that it might last until the eel reaches the sea, over a 'migration period' (a period when conditions on successive nights are suitable for migration) of perhaps a week, light or some other factor inhibiting the migration by day and darkness allowing it to continue on successive nights, or the eel might need restimulating anew each night by the trigger factor. The evidence, given below, is at present in favour of stimulation lasting over a 'migration period'.

If the effect of the stimulation lasts, this may explain the capture of eels on dark nights when there is no flood. If flood is the initial stimulus it seems that the effect must last several nights at least, for there are generally far too few nights of rising floods during the eel season to allow the eel to reach the sea if the active state were only induced by a rising flood and lasted for only one night. Also floods do not seem to be so necessary for the migration later in the season and nearer the sea. Nearer the sea the eel runs tend to occur at dark of moon periods with greater regularity. Fig. 3 shows clearly that whereas at Dalemain, about 50 miles from the sea, eels continued to run throughout the full moon period early in the season, at Newby Bridge, about 6 miles from the sea, the occurrence of eel runs was well defined by the phase of the moon. Yellow eels are attracted by light (personal observations) and lights are used when 'bobbing' for these eels with worsted threads as bait. The negatively phototactic response of the silver eel appears to develop together with the increase in eye size which marks the change from yellow to silver form. Silver eels later in the season and nearer the sea are likely to be more sensitive to light than those which are just completing the metamorphosis and starting the seaward journey. In spite of this, however, particularly large numbers of eels are caught when there are floods even in traps quite near the sea. This suggests that many of the eels are stirred to renewed activity by the flood, rather than that they represent a wave of eels stimulated when upstream, travelling at the same speed and arriving at the traps near the sea in one party at a fixed period after the flood. In traps near the sea it is unlikely that the sudden increases in numbers of eels trapped are due to eels which have just reached a minimum stage of preparedness and are being activated by the flood for the first time.

Thus it seems that activity due to the initial stimulus does not last throughout the whole journey to the sea, but that the majority of the eels probably need reactivating several times. That the activity lasts for a varying length of time in different eels is also indicated by the behaviour of the eels in the artificial runs, when some continued downstream and some did not, and by the variability of behaviour in the laboratory. It is quite possible that the inhibiting effect of light may be cumulative and may counteract the activity due to the flood stimulus. The length of time after the initial stimulus that this activity would last probably depends on the degree of preparedness of the eel and its consequent responsiveness to the original stimulus, the intensity of the original stimulus, and possibly a cumulative effect of light as an inhibiting factor.

(*b*) *The behaviour of migrating silver eels*

There is considerable circumstantial evidence that the silver eel has to be stimulated into an extremely active 'migration mood' before it will migrate. This evidence comes from:

(1) Attempts to induce artificial runs of eels in the field (see p. 284). These attempts were not very successful as twenty-six out of forty eels released were not retrapped during the night that they were released and must have gone to ground or swum back up into the lake. As these eels had all been migrating downstream actively a night or so previously, this shows that 'roused' and 'unroused' silver eels behave differently, that this difference in behaviour is influenced by external conditions, and that there is variation in the behaviour of individual eels.

(2) The release of marked eels (see p. 284). Of twenty marked eels returned to the outflow end of Esthwaite only four were recaptured and none of these was recaught on the first night of the next big flood, 20 days after the marked eels were returned to the lake. This suggests either that there had been undirected wandering during these 20 days, or that fresh 'physiological preparation' for the new migration was needed. Disturbance, such as exposure to light while marking, might have affected these eels though outwardly they did not appear upset by the process, and marking, to find the rate of migration, has been used in the Baltic with some success (Trybom & Schneider 1908). It seems improbable that these healthy eels, which were already migrating and returned to the lake the same day that they were captured and marked, would remain inactive under such eel-activating conditions as occurred on the night of 29–30 August 1943. The four eels recaptured, though originally caught the same night and returned to the lake in one batch, were not retrapped the same night; there is no evidence of any social relationship between the migrating eels.

(3) Responses to lighting experiments in the field. Results from lighting experiments also indicated that the activity of the silver eels was affected by external conditions. For example, on 8 and 29 August 1943 the percentage of the eels deflected by artificial light decreased as the night advanced (Fig. 5). On these two nights over eighty eels were caught, there was a scarcely rising flood and a faint intermittent drizzle of rain. On 30 August, however, the most stormy night with a rapidly rising flood, 185 eels were caught; they were notably more active than usual and continued to respond to the artificial light throughout the night (Table 4 and Fig. 5). Throughout the lighting experiments the eels were noticeably more active and more difficult to handle on dark stormy nights. In addition to general variation in activity in all the migrating eels correlated with weather conditions some variation between individual eels was noted. This was to be expected as some eels may have swum much farther than others before entering the trap, and in big floods, particularly in the early part of the season, eels not yet fully silver, and still feeding (i.e. the gut contained food), were taken along with the fully silver eels. From the behaviour of these half-silver eels it was obvious that they were migrating actively and had not merely been washed down the beck into the trap.

(4) Activity of eels in the laboratory. Throughout the laboratory experiments, too, there was much individual variation from eel to eel in response to current and light.

Eels from the Cunsey Beck traps brought straight to the laboratory and run in the artificial river the same night swam headfirst downstream more actively that at any other trials in the river. There was also a difference in the behaviour of these eels which appeared to be related to the number of eels running in the field on the night that they were trapped and the stage of the migration period; the eels remained active longer in the artificial river on the night when more eels were migrating in the field, and eels taken after several days of flood were less active. Eels kept in still-water tanks in the laboratory were roused to activity and leapt out of the tanks on the same nights that eels were known to be migrating in the field, and during the same dark hours of the night. This is particularly interesting as in these tanks there was no question of floods initiating the activity. Fall in temperature (see p. 298), darkness of the night, and barometric pressure appeared to be the only factors common to the field, and these tanks which might account for this behaviour. The only records of barometric pressure were for the early part of the 1944 season and were not sufficient to suggest that this factor may be important. The peculiar active state of the eel may last throughout the night until the first sign of dawn, particularly on wild stormy nights with a rapidly rising flood. Observations on less stormy nights, however, suggest that eels are most active in the early hours of the night; the decrease in activity may be due to fatigue.

Evidence on whether eels congregate near a lake outflow and there await conditions suitable for the downstream migration is conflicting. At the Cunsey Beck the eels generally arrived immediately it was dark and the migration often took place for only a few hours each night; also the greatest catches were on rising floods and catches fell off on subsequent nights even when the river remained at a high level. This suggests that the eels which are in the right physiological state for migration congregate near the lake outflow and there await a stimulus to travel downstream. The silver eels evidently congregate near the outflow of the River Bann from Lough Neagh in Northern Ireland as seines are used, illicitly, to catch them there (Frost 1950). There are few other records of silvering eels being caught in lakes. Petersen (1894) and Rodolico (1933) both watched the silvering process in live boxes or tanks, but very few silvering eels have been caught in the field except on migration. Walter (1910) states that Bellini saw very few silvering in his experimental ponds and that Bellini suggested that the eel buries itself in the mud during the metamorphosis. There is also evidence that eels do not always congregate near a lake outflow. At Cunsey Beck the migration was not confined to the early hours of the night when the river was rising rapidly, and catches during three consecutive nights (Fig. 5*b–d*) showed that the maximum number of eels trapped per hour was earlier on each successive night. This suggests that the eels were travelling down the lake on the earlier 2 nights and it stresses the effect of the flood in initiating migration. At Corby Castle, which is not near any lake outflow, the migration also took place during the early hours of the night and for only a few hours except on a rising flood; information collected by Mr F. T. K. Pentelow of the Ministry of Agriculture and Fisheries suggests that this is the case on many rivers. Thus it seems that some eels in a lake may congregate near the outflow and there await a flood, though not all eels do so.

Field observations showed that migrating silver eels swim headfirst downstream, so they travel faster than the water current. Trapping experiments at Cunsey Beck in 1941

and 1942 (p. 283) suggest that most eels migrate near the bottom rather than near the surface in these rivers, though Petersen (1906) observed some silver eels migrating near the surface on dark nights in the Baltic. Whether eels ever descend tail-first, as salmon smolts are said to do when in very turbulent water, is not known. A non-migrating eel probably maintains its position in flowing water when in the light by optical fixation. The eel is, however, mainly a nocturnal animal. Gray (1937) has shown that blind eels respond to curvilinear water movements, which are probably perceived through the semicircular canals. Wunder (1927) has shown the eel to be very sensitive to mechanical disturbances in the water, which are perhaps perceived through the lateral line. These responses, together with direct contact, would enable an eel to maintain its position in flowing water in the dark as long as it kept fairly near to the bottom or to static objects in the water. In the artificial river the curve between the two straight channels and slight eddies along the central wall probably enabled an eel to maintain its position facing upstream in complete darkness, even when not actually in contact with the sides or bottom of the tank.

The time that upstream-swimming eels could continue to swim against the current was proportional to the strength of the current. This is also clear from Fig. 13 in which the cumulative totals of eels trapped after successive 5 min. periods are plotted for three different water speeds. Runs in total darkness and with a light barrier both showed this effect. Actual times of maintaining their position against the current varied very much from eel to eel, and with the position of the eel in the tank; some eels were able to get into the relatively slow-flowing water near the junction of the tank wall and the bottom, in which cases results were misleading and had to be disregarded. In the dark-light choice experiments, some eels were timed with a stop-watch as they swam round the tank, a distance of 34 ft. The average for five consecutive 'runs' by one active eel swimming headfirst downstream was 14 sec., ranging from 12·7 to 16·3 sec. for the 34 ft. swim. This eel was therefore covering ground at the rate of 2·43 ft./sec.; and as it had the help of a 1·7 ft./sec. current down the two 14 ft. stretches it was swimming about 1·0 ft./sec. faster than the current. Other eels swam with the stream at a similar speed.

In the Baltic, Trybom & Schneider (1908) found from marking experiments a maximum movement of silver eels of 50 km. in 24 hr., which is 1·9 ft./sec. assuming continuous travel, but more often about 15 km. were covered in 24 hr., which is 0·57 ft./sec. assuming continuous travel. In the field the speed of swimming would be modified by the nature of the stream bed, as eddies from a rocky bottom might give the eels more shelter from the current than they had in the smooth experimental channel. At Cunsey Beck in 1943 the lights still had effect in water flowing at 2·5 ft./sec. At Nibthwaite, although no water speeds were measured, the lights had a highly significant effect in 'low' flood, but no effect when the water was higher and flow swifter (see Table 9).

The behaviour of salmon smolts (*Salmo salar* L.) when migrating to the sea provides an interesting comparison with eel migration. Allen (1944) studying the smolt migration in the Thurso River in 1938 found waves of activity apparently due to a stimulus to active migration travelling down the river; this stimulus he believed to be a rise in water-level. Allen suggested that there is a great variation between individual

smolts in the degree to which they have developed their migratory reactions, and also that the passage of actively migrating smolts would possibly act as a stimulus to smolts migrating slowly or on the verge of migration. It seems quite likely that this will also occur in the eel, and that the numbers of eels migrating may affect their activity. The eels are certainly more active when many are migrating, but whether this is due to the direct effect of external conditions or is the effect of the many eels migrating, or both, cannot be decided on the present data. Pritchard (1944) working on the migration of the fry of Pacific pink salmon (*Oncorhynchus gorbuscha* (Walbaum)) found that migration to the sea was usually swift and vigorous but that movement was limited to the hours of darkness and slowed by direct moonlight. Pritchard concluded that flood does not initiate the migration but causes fry already in motion to proceed more quickly. He found that small temperature variations had little effect.

(*c*) *Experiments on the responses of silver eels to light*

Experiments in the field and laboratory on the effect of light on silver eels have shown that a light barrier will stop the migration, and that migrating silver eels may be deflected to the side of the stream by light. Whether the extreme activity associated with the 'migration mood' raises or lowers the threshold of response to other factors such as light was considered. Results from light experiments on three consecutive nights at Cunsey Beck (Fig. 5*b–d*) showed that the lights had most effect when the eels were most active, suggesting that the threshold of response to light is lowered when the eels are in 'migration mood'. On the other hand, as mentioned on p. 292, among the small yellow eels, 'snigs', trapped in ones and twos throughout the experiments, the proportion trapped on the dark side of the stream was higher than for silver eels. This might suggest that the silver eels were responding *less* actively, or paying less attention to the lights, than these snigs, particularly as the eye structure indicates that the silver eels should be more sensitive to light than the snigs (Walls 1942, p. 405). The explanation may, however, be that the snigs keep closer to the bottom of the beck away from the current so may be able to respond to the light in a more leisurely and controlled manner.

During the 1943 season the Cunsey Beck traps were designed to catch all the silver males, which escape through many of the commercial eel traps because they are much smaller than the females. At Cunsey Beck in 1943 only twenty (3%) male to 613 female silver eels were taken scattered throughout the season. Twelve were taken on the dark side and seven on the lit side. At Nibthwaite and Dalemain the percentage of males seemed much higher but was not determined. The eye of the fully silver male eel is relatively larger than that of the female (Sivertsen 1938, and personal observations), but there is no reason to suppose that there is a great difference in response to light between male and female silver eels at this stage of their journey. Petersen (1906) mentions that the silver eels caught during his light experiments were nearly all males; this was probably because he was working nearer the sea, and as is well known, male eels are often found near the estuaries of rivers, whereas females tend to predominate in waters well away from the sea (Frost 1945 and 1950).

At Cunsey Beck a light barrier of 5·3 or 0·25 c.p. across the outflow of the stream from the lake had a highly significant effect in checking the eel migration. Half-hour

periods were, however, the longest tried, and it is not known for how long such a light barrier would continue to be effective as no opportunity occurred to test whether the eels could be held up for longer. At the Cunsey Beck site the eels would probably see some light before they left the relatively slow-flowing water at the end of the lake, and such a barrier might not be effective in checking the run for long in a fast current where they had less time to react to the lights. Cunsey Beck results for 1942 (Table 8) showed that lights shining vertically downward into the water to make a continuous light path across the stream had a highly significant effect in deflecting the eels. The lights had, however, no effect on a few nights of high flood in 1942. On these particular nights the lights were uncapped and the very rapid current swung the lights almost horizontal so that they were shining downstream, only the surface waters were illuminated, and little light would be visible to the downstream-swimming eels. The Cunsey Beck experiments in 1943 and 1944 (Table 8) showed that underwater lights directed upstream had a greater effect on the eels. This was confirmed at Nibthwaite where the lights only had a significant effect when they were directed upstream (Table 10). These upstream-shining lights would appear to the eels as a series of bright blobs rather than a continuous light path; they gave the eels a longer warning which was probably particularly necessary when the current speed was high. Owing to the restricted space in the artificial river no evidence on the effect of direction of light was gained from laboratory experiments.

It was noted that dimming of the lights due to any cause such as accumulators running down, or algal growth on the lights, did not appear to affect the result. When tested in tanks of still water the eels appeared to be sensitive to much smaller intensities than were used in any field experiments, intensities too small for the human eye to watch the eels' response. At Cunsey Beck (Table 7) 5 c.p. lights appeared slightly more effective than 0·25 c.p. lights. The difference was not, however, statistically significant. In the artificial river the results given in Table 12 and Fig. 13 show that no significant difference in effect was found between light barriers giving 67·95 and 0·075 c.p. In the dark or lit passage trials in the artificial river results concerning the effect of lights of different intensities were conflicting. Brighter lights appeared to check the number of downstream runs; e.g. with a 21·4 c.p. light eight eels totalled twenty-seven runs before turning upstream against the current, an average of 3·2 runs per eel, whereas with a 4·0 c.p. light eight eels totalled sixty-four runs, an average of 8 runs per eel. This suggested that the brighter light was the more effective in preventing the downstream run. On the other hand, those eels which did proceed downstream when the bright light was used did not choose the dark side more often than the lit one. This may have been due to selection by light, the most light-sensitive eels staying upstream, or to the brighter light having less shock effect as it probably warned the eels when they were farther upstream than did the dimmer lights. Therefore, although there was some indication in the field that a brighter light might be more effective, it seems equally possible that once above a certain low threshold, lower than any used here, the intensity may not be very important in determining the reaction of the eel and is probably less important than the shock effect of the light.

There were indications in early experiments in still water that silver eels are most sensitive to the blue-green end of the spectrum. The anatomy of the silver eel's eye

also suggests this, as it is particularly rich in rods; rods are used when the eye is dark-adapted and are most sensitive to the blue-green end of the spectrum and least sensitive to red light (Walls 1942, p. 76). No further experiments with coloured lights were made. Birge & Juday (1930) have shown that, although light at the blue end of the spectrum penetrates farther than the red in clear water, the blue light is more affected than the red by suspended particles and colour in the water.

(*d*) *Practical considerations for the deflexion of eels by light*

From the practical point of view it has been shown that under certain conditions the silver eel migration may be checked or the eels deflected into traps by means of light, and that light is useful to prevent the escape of eels while changing traps and nets. The field experiments described here were, however, restricted by wartime conditions. Should any further experiments be planned now that these restrictions have been removed the following points, gained from experience in these experiments, should be helpful.

All the lights must be easily accessible for cleaning and repairs. Algae and *Simulium* larvae and pupae had to be removed from the lights at frequent intervals, and though in theory these lights could be drawn to the river bank for cleaning, in practice the wires generally jammed. Good anchorages were difficult to find or fix near river banks, and the weight of the equipment used, suspended from aerial wires, limited the lengths of span of the light barrier. Sites with sudden and drastic rises in water-level and with much large débris, such as tree trunks, likely to come down in a flood, are to be avoided; the buffering effect of a lake is helpful.

The angle of the light barrier to the current must depend on conditions prevailing at the particular site, but the conflicting facts are that a long gradual warning will be necessary in a fast current, and that the shock effect is most important for checking or deflecting the eels. At Cunsey Beck in 1943 (Table 8) a short line of lights at 35° to the current deflected slightly more eels than a longer line at 12° or than both lines together, as can be seen from the percentage of eels trapped on the dark side, though this difference was probably not statistically significant. On the Cunsey Beck the lights proved effective in water up to 4 ft. deep and with a current speed of 2·5 ft./sec. It has been shown that lights of 5 and 0·7 c.p. will deflect eels in fairly clear water, but the evidence whether brighter lights would be more effective is conflicting. In turbid water brighter lights would probably be necessary; it is the blue end of the spectrum which is likely to prove most effective, even though this is just the light which is most affected by turbidity.

(*e*) *Conclusions*

The extreme activity of migrating silver eels can be correlated with conditions of water-level and darkness. Bearing in mind four aspects of any migration, the preparation, the trigger stimulus, the guiding forces, and factors stopping the migration, it seems that silver eel runs may be influenced in the following ways:

(i) The physiological preparation is associated with the change from yellow to silver eel; this change is not considered here. When this metamorphosis is complete some external stimulus is necessary to activate the eels to migrate. The responsiveness

will depend on the degree of preparedness, and since this varies it probably determines the amount of the external stimulus necessary to initiate the migration.

(ii) It seems that flood or some associated factor provides the initial stimulus to migrate to all silver eels. It is suggested that flood may affect the eels through a fall in water temperature, but flood may also represent a general index of many coincident physical and chemical factors which it has not been in the scope of this work to consider. The phase of the moon appears to affect the eel through the inhibiting action of light, rather than darkness or any periodic effect stimulating the eels to run.

(iii) The guiding forces directing the eel are still obscure, though it seems likely that floods or some associated factor may help to guide eels to a lake outflow. In rivers floods probably have a mechanical action in speeding the eels seawards.

(iv) The effect of the initial trigger stimulus probably lasts for several nights at least, the eels running continuously, except when inhibited by light as during the day and on bright moonlight nights, until the effect of the stimulus wears off. Light will have a relatively greater effect if the eels are in clear or shallow water. The duration of the activity due to a flood stimulus probably depends on the degree of preparedness of the eel and consequently its responsiveness to the original stimulus, the intensity of this original stimulus, and possibly also a cumulative effect of light as an inhibiting factor. Except for eels living in a short river flowing directly to the sea it seems unlikely that the original stimulus lasts for the whole journey, and the eel may need restimulating several times. It seems, therefore, that the eels are checked by day and on bright nights by light, and migration is suspended when the effect of the trigger stimulus wears off until the eels are restimulated, probably by further floods.

Laboratory experiments suggested that once the shock effect of light wears off silver eels respond photokinetically instead of negatively phototactically; this response may be part of the mechanism whereby the migrating eels cease running and are led to hide away during the daylight hours.

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SUMMARY

1. Observations on the conditions, particularly floods and the phase of the moon, which affect the seaward migration of silver eels were collected for three years from six field sites in the English Lake District.

2. These observations confirmed that silver eel runs occur only between late summer and early winter. The higher upstream the eels the earlier in the season they are trapped.

3. The migration was confined to very few nights, on which large numbers of silver eels travelled seawards; eels ran on the same nights at widely separated sites.

4. Most eels migrated when floods coincided with moonless periods. Few eels ran when there was a full moon; the run could be checked experimentally by artificial light. The start of the eel season was delayed until there was a flood, after which some eels ran on dark nights when there was no flood. The greatest catches were made on rising floods. Weather conditions were not as important as floods in determining whether eel runs occurred.

5. Eels tended to run in the early hours of the night except on a rising flood. Evidence whether eels congregate near a lake outflow before migrating downstream was inconclusive.

6. Attempts to induce runs of eels and to re-trap marked eels were not very successful, but both contributed evidence that silver eels have to be stimulated into a 'migration mood', a state of extreme activity, before they will migrate. This mood appeared to be related to conditions of flood, possibly fall in temperature and darkness of the night. Eels kept in tanks in the laboratory were particularly active the same nights that eels were migrating in the field.

7. Experiments in the field and laboratory have shown that the downstream migration of silver eels may be (*a*) checked, and (*b*) deflected by lights. At Cunsey Beck a series of underwater lights stopped the run of eels for half-hour periods. For the deflexion of eels into traps at the side of a river underwater lights must be thrown well upstream; lights shining vertically downward into the water are less effective. Upstream-shining lights of about 5 and 0·7 c.p. were effective in Cunsey Beck; evidence whether brighter lights would deflect more eels is conflicting. The extreme activity of the silver eel associated with migration appears to lower the threshold of response to light, artificial lights having most effect on the nights when the eels were most active. There is no reason to believe that the response to light differs according to the sex of the eel.

8. In an artificial river in the laboratory the downstream swim was delayed by light and eels chose a dark channel in preference to a lit one; there was evidence from laboratory experiments that once the shock effect of the light wore off the eels responded photokinetically instead of negatively phototactically.

9. In the artificial river the eels swam upstream against a flow of 1·1 ft./sec., but tired rapidly against a current of 1·7 ft./sec.

10. It was concluded that flood, or some associated factor, possibly fall in water temperature, acts as a trigger stimulus starting the downstream migration. Eels then run continuously, except when inhibited by light during the day and on nights with bright moonlight or starlight, until the effect of the activating stimulus wears off. Most eels will probably need restimulating several times before they reach the sea.

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NOTE ADDED IN PROOF

Since going to press an abstract of a paper by D. E. van Drimmelen on 'Vangst van Schieraal met Behulp van Licht' ('The use of light in the catching of eels') *Visserijnieuws*, **3**, No. 12, 1951) has been seen in *World Fisheries Abstracts* **3**, No. 2, 1952. Van Drimmelen tried the effect of two 250 W lamps, on opposite sides of a canal, on fyke net catches of migrating eels. This showed that the fyke nets farthest upstream from the lights caught most eels.

GAUSE'S HYPOTHESIS: AN EXAMINATION

By O. GILBERT*, T. B. REYNOLDSON and J. HOBART
Department of Zoology, University College of North Wales, Bangor

Two recent papers (Bagenal 1951; Williams 1951) have focused attention once more on what is known as Gause's hypothesis. Both these papers are the outcome of the British Ecological Society's 1944 Symposium on the ecology of closely related species. Gause's hypothesis as stated in the report of this symposium (Anon. 1944) reads 'two species with similar ecology cannot live together in the same place'. Lack (1945) states 'Gause contends that two species with similar ecology cannot live in the same area'. In addition, Lack (1947) has three statements of the hypothesis attributed to Gause: p. 62, 'two species with similar ecology cannot live in the same region'; p. 140, 'two animal species with the same ecology cannot live in the same region'; p. 142, 'two species with similar ecology cannot live together'. Allee, Emerson, Park, Park & Schmidt (1949, p. 660) state 'Gause's thesis' as 'two species with identical ecology cannot persist together in the same area'. Williamson (1949) and Green (1951) give the so-called Gause's contention in a different way: 'no two species in the same habitat have the same ecology'.

Diver's remarks (Anon. 1944) at the Symposium, although unfortunately not reported in full, appear to have been very apposite in pointing out that the hypothesis under discussion was notable for what it left unsaid. Indeed this is so true that many of the terms used in the statements quoted are so imprecise that one's understanding of them must be subjective. Diver stressed the difficulty of defining 'similar ecology'. As it is used in the above statements, the expression is objectively meaningless. Subjectively it appears to indicate that two species have a number of ecological requirements in common. To try to define the exact level which this similarity implies however, resembles trying to decide how many hairs must be lost for a head to be described as bald. There is also a danger of a circular process here, in that 'similar ecology' may be used to imply unwittingly a state in which of two species 'living together' only one species is able to maintain itself. However, in a sense, all organisms which have a mutual environmental requirement in regard to one factor, are in regard to that factor ecologically similar, e.g. all sessile animals are ecologically similar in their requirement of a substrate. In some cases the coincidence of requirements will be greater than in others; it is possible to visualize a complete series from one mutal requirement to all the environmental requirements of two species being common to both. Close taxonomic relationship is not necessarily involved in this conception of ecological similarity. The use of the term 'same ecology' in two of the statements presents another problem. If the word 'same' as used here is synonomous with 'similar', the above remarks apply also. On the other hand, 'same ecology' may imply 'identical ecology', which is the term used by Allee *et al.* (1949). It is pertinent to inquire whether species which are truly ecologically identical, surely an improbable state, would be differentiated by any ecological process!

* Holder of a Nature Conservancy Research Studentship.

Gause himself, in the work usually quoted as containing the hypothesis (Gause 1934*b*) and also in Gause (1934*a*), the paper cited by Allee *et al.* (1949), makes it quite clear that the experiments relevant to this hypothesis concern *competing* organisms. It would appear, however, that the framers of the statements under discussion, by omitting to mention competition either hold that it is not a relevant factor, or hold that all species with 'similar ecology' will compete if a vague temporal and spatial relationship, viz. living together, exists between them. It should be mentioned that Lack (1946) does state 'Gause's thesis' as 'when two species compete for the same food supply one must eliminate the other'. However, Hutchinson (1948) points out that continual oscillations in the environmental variables may continually reverse the direction of competition. He also points out that external factors, e.g. predators, may so rarefy mixed populations that the environmental possibilities are never exploited, and so two potential competitors never come into competition (see also Crombie 1947, p. 47).

The spatial limits implied by living in the same place, living together, etc., as used in the various quotations, are not clear. It seems better to define the locus of interaction of two species without using these phrases. The type of interaction implied might be expressed by considering animals with a mutual density-dependent requirement fulfilling this requirement from the same source. As well as the spatial aspect time also must be considered, as Bagenal (1951) emphasizes. The decline of a population through competition will have duration, and even if the decline leads to the ultimate extinction of a population, there will be a period during which the competitors will 'live together'. That this aspect is recognized by Allee *et al.* (1949) is shown by their use of the word 'persist' (see also Lack 1946). If the rate of decline is slow enough, mutations occurring and spreading through a population may accentuate, ease or reverse the course of competition, or bring about an end of competition between the two species (see also Crombie 1947, p. 47). Moreover, a temporary change of habit under adverse conditions may alter the relationship between two populations. It should be noted in passing that two interacting populations need not be contemporaneous. The legacy of conditions left by a population of one species may affect a population of the same or a second species which comes later. But this aspect is not confined to species with a mutual density-dependent environmental requirement and will not be discussed further.

Although individual organisms obviously play their part in interspecific competition, the course of competition can be ascertained only by a consideration of changes in the relative sizes of populations. Application of this idea is made difficult by different environmental requirements at various stages in the life-history. Moreover, competition may be restricted to certain areas within the common range of two populations, and where competition does occur, it may take different courses in these separate areas, and indeed involve different factors. These facts allow the effect of adverse competition in respect of one of the species in a particular area to be offset by immigrants derived from more favourable areas. In a limited system such as Gause used the concept of population as a local interbreeding unit (Mayr 1948) is easily applied. However, when one tries to extrapolate from culture to field conditions, the delimitation of a population becomes a stumbling block. This problem emphasizes how difficult it is

to apply ideas gained from laboratory experiments to the complex conditions existing in the field.

Gause (1934*a*, 1934*b*) draws no general conclusions from his experiments, and moreover, makes no statement which resembles any wording of the hypothesis which has arisen bearing his name. He is content to show that in his cultures the equations developed theoretically by Haldane (1924), Volterra (1926), and Lotka (1932) for competing organisms appear to hold. On pages 19–20 of his book (Gause 1934*b*) however, he quotes the observations of Formosov on Black Sea terns showing that the different species are not dependent on the same source of food; observations of this type have since been paralleled for other animals, mainly birds, and given as supporting evidence for 'Gause's hypothesis'. However, as this hypothesis is concerned with ecologically similar animals not living together—whatever this means—it is difficult to derive supporting evidence from ecologically different animals which do live together. The observations do, however, support a derivative hypothesis of Darwinism that, in a population of a species, mechanisms which reduce competition between it and populations of other species tend to persist.

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* Original not consulted.

REVIEWS

THE HABITS OF MOSQUITOES

R. C. Muirhead-Thomson (1951). *Mosquito Behaviour in Relation to Malaria Transmission and Control in the Tropics.* Pp. viii + 219; 16 plates; 22 text-figures. London: Arnold. Price 30*s*.

This is an important contribution to animal ecology. That would be true even if the extensive work that has been done on mosquitoes were well known to animal ecologists. In fact it is not, as a glance at the indexes of any of the standard books will show. *The Principles of Animal Ecology*, the recent large American publication, has but four references to *Anopheles* (indexed under mosquitoes) in its 729 pages; Elton's *Animal Ecology* has one. This neglect of a group that has been studied more thoroughly than any in the world is not hard to account for; most of the work has been published in medical journals or even in journals devoted entirely to malaria, and much of it is mixed up with practical details of no interest to the general student. This mound of material has daunted even malariologists of late years, and Dr Muirhead-Thomson has done a great service in sifting it and collating the valuable parts.

In 1898, when Ross demonstrated that it was they who carried malaria parasites from one vertebrate host to another, mosquitoes ceased to be just another family of insects awaiting the attention of some museum specialist, and became objects of concern to everyone in the tropics. Scientific attention was turned upon them, discovery followed discovery, and the field of investigation expanded rapidly and in many directions during the first few years of the present century: the Italians showed that only the genus *Anopheles* transmits the malaria parasite; Christophers and Stephens showed that only some species in that genus are serious vectors; Gorgas made possible the building of the Panama Canal by his anti-mosquito measures; and great developments in Malaya followed Watson's anti-malaria campaign.

Both in America and in Malaya, effort was concentrated against the vector, and other species were ignored, a policy which later received the rather curious name 'species sanitation'. It was evident from the earliest days that malaria control was an ecological problem, and immediately attention was directed to what is always the first step in an ecological problem—thorough taxonomic study.

After the first few hectic years there began an era of steady, less spectacular research which can be divided very roughly into periods, each dominated by a different idea. The successes in Panama and Malaya had been against larvae, and it was on this stage that early interest focused. Every species was confined to a definite habitat; some places produced dangerous species, others harmless ones. Could one type of breeding-place be turned into the other? First it was necessary to discover exactly what the differences between the breeding-places were, and the literature abounds in lists of algae, *p*H records, chemical analyses, and so on. But an exact definition of the habitat of any one species proved as elusive as the elixir; though that is an unkind analogy, for it would be ungracious not to recognize the value of the contributions that earlier workers made.

This tendency to regard the larva as a wholly aquatic creature and to ignore the part its mother might play in establishing it in a given type of place gradually gave way to an outlook that treated all the stages in a mosquito's life-history as parts of a whole, and took more interest in the adult's behaviour. It became essential to know more about the habits of the adults when, in the early thirties, their destruction with pyrethrum sprays came into fashion, and the importance of the subject was underlined by the coming of DDT. Many campaigns using this substance were started after the war, and there were some striking successes. There were also failures. Muirhead-Thomson quotes four cases in which results were disappointing and could doubtless have quoted more, had he not confined himself to those of which accounts have been published. It is now clear that anyone who launches a DDT campaign without first obtaining detailed information about how the species he is attacking behaves is embarking on a gamble. The study of the behaviour of the adult mosquito—where it bites, when it bites, where it rests, and so on—is the idea dominating practical investigations to-day.

Dr Muirhead-Thomson is not a medical man; he is a trained scientist with a scientist's outlook, and has written a book which, notwithstanding its title, will appeal to a wide range of

ecologists. 'Behaviour' is interpreted in the widest sense, and the book could have been called 'Mosquito Ecology', or, more accurately, '*Anopheles* Ecology' equally well. Muirhead-Thomson's concern with malaria transmission and mosquito control gives him an objective that stiffens the whole book and provides a focal point that it might have lacked if written from a purely academic standpoint.

There is an introduction and then two hundred pages of text divided into two parts with six chapters each. The first four chapters deal with swarming and mating habits, feeding and egg-development, longevity, time of biting and other activities during the night, the choice of resting places for the day, and the selection of an animal to feed on. These chapters give straightforward accounts of what is known, dwell on certain facts that were thought to be known but which cannot be accepted when examined critically, and indicate lines that future investigation might profitably take. The whole book is concerned only with the genus *Anopheles*. Little or nothing is known about most species, and, except for an odd fact here or there, the book is about the dozen or so species that are serious vectors. Of necessity it must jump rather suddenly from one to another because different workers have been interested in different attributes of the species they have studied, and for no single one are there data under all the heads named above. Chapter 5 discusses temperature, humidity and light, the first two mainly from the point of view of differences between the readings in standard screens and in places where mosquitoes occur. It is a little disappointing that the data about temperature as the factor limiting the range of mosquitoes is not reviewed here. Chapter 6 describes mosquito behaviour in places where insecticides have been sprayed.

The second part of the book has a more coherent theme, and any ecologist who has ever given thought to the problem of why a given species is confined to particular habitat conditions should find it fascinating. Probably the most thorough single contribution to this problem is that made by the author himself, when working on *A. minimus* in Assam before the war, and this provides a connecting theme through all the chapters but the last. Data on other species are brought in where relevant. The approach is a synthesis of field observation, field experiment, and laboratory experiment on both adults and larvae. Muirhead-Thomson is less sceptical about laboratory experiments than Bates, who wonders whether any mosquito which has become aware that it is confined within a cage reacts quite as a wild one would. The last chapter is about species that breed in brackish waters, and here ecology has not proceeded far beyond the descriptive stage.

There are places where the style may jar on the purist, but Muirhead-Thomson selects and marshalls his facts well and expounds his ideas clearly. Two small suggestions for the next edition are a decision whether to include the generic initial or not, and the omission of the Indian words on pp. 29 and 164. To those who have been to India the word 'pukka' and its opposite 'kutcha' convey a meaning that cannot be conveyed by any single English adjective, but the latter at least is likely to have no meaning for others. They will also be puzzled by the use of the word 'tank', which in India is an artificial pond. There are twenty-two black-and-white photographs, most of which do not add greatly to the value of the book. A photograph can never convey the impression of a habitat that the eye gains, for it cannot in one moment explore a wide background and in the next concentrate on a detail while retaining a picture of the whole scene.

Three other important books on malaria and mosquitoes have appeared since the war, and it is meet that their relation to this one should be noticed. Russell, West and Manwell's (1946) *Practical Malariology* (684 pp.) is overshadowed, at least for those not directly concerned with malaria control, by Boyd's (1949) *Malariology*, a symposium with sixty-five illustrious contributors and 1643 pages. The ecologist may find in them much that is of interest about *Plasmodium*, the three common species of which, although they provide the most striking example of closely related species occupying the same ecological niche, have not often been mentioned in the discussions on that topic, which have been frequent in recent years. The subject on which Muirhead-Thomson has written his book is, however, covered in quite a short space: a chapter of some twenty-five pages on mosquito ecology by Bates, with some relevant information in chapters of similar length on physiology by Wigglesworth, and life-history by Buxton and Leeson.

The fourth, Bates, M. (1949), *The Natural History of Mosquitoes* (New York, Macmillan), is a book of much greater value to readers of this *Journal*, and one that is incidentally written in a light and attractive style shunning, and indeed mocking, the complex verbiage that makes some American books hard reading for Britons and some ecological books hard reading for everybody. It is about one-third as long again as Muirhead-Thomson's but it covers a much

wider field, including all mosquitoes, not only *Anopheles*, and dealing with a number of topics not mentioned in *Mosquito Behaviour*. The relative value and importance of the two books depend on the reader's interests: if he is an omnivorous naturalist interested in the odd and the bizarre as well as the general principle, he will prefer Bates's book; if he is interested in the details of behaviour in a single genus, or in the problem of how different species come to occupy different habitats, he will prefer Muirhead-Thomson's. I doubt if anyone who reads both books will regret it.

T. T. MACAN

TROUT BIOMASS AND PRODUCTION

K. R. Allen (1951). *The Horokiwi Stream: A Study of a Trout Population.* N.Z. Marine Department Fisheries Bulletin, No. 10. Pp. 231. Wellington.

One field of population ecology has concerned itself with not only the numbers of organisms but also their total weight or *biomass*. As well as the total biomass of a species present at any one time the total amount of material becoming embodied in that species over a period of time, the *production*, is obviously of fundamental importance. If these concepts are extended from one species to include its food, its predators, and its competitors, knowledge will be gained on the basic quantitative dynamic structure of the community. This is obviously of great value not only for the development of fundamental ecological understanding but also for the efficient economic ultilization of animal populations. It is not surprising therefore that fishery biologists have frequently attempted to obtain some measure of production, from estimates of the populations, mortality-rates and growth-rates of fish species, and to relate this to rates of cropping, and available food supplies. The success of these attempts has largely turned upon the success with which the basic data can be obtained simultaneously in a relatively complete state, for one fairly discrete population. Allen's study of the trout in the Horokiwi stream is another attempt of this kind. It is distinguished, however, by the success with which the basic data have been collected, by the fact that limits of accuracy have been estimated for each of these basic data, and by the stimulating nature of the results obtained. It may thus prove to be one of the most important papers yet published in this field.

In spite of the unequalled and world-wide recreational importance of the brown trout, this is the first time for any trout population that data of this completeness have been collected and efficiently analysed to yield the basic information on stock, production and crop. The investigation was planned to investigate these fundamental concepts and in particular their relationship to the food supply. The latter, consisting almost entirely of bottom fauna, was estimated as population and biomass by one of the usual sampling methods. As however the data on the trout revealed the fundamental superiority of production over simple biomass as an ecological parameter, and as the annual food consumption by the trout is shown to have been as much as 40 to 150 times the biomass of bottom fauna at any one time, significant conclusions on the food supply must await estimates of the production of the bottom fauna. Thus it can be said at the outset that the aims of the investigation have been amply fulfilled except as regards the bottom fauna where partial fulfilment has raised new problems.

The Horokiwi stream is some 10 miles long, and is a typical small New Zealand river with the brown trout (introduced some 70 years ago) as the dominant fish species. The investigation was over a period of two years, the different year-classes contributing to the study of trout of different ages, thus allowing a 'composite' year-class to be followed throughout its full life. The paper consists of four main parts as well as an introduction, conclusions and appendices of data. The first describes the physical features of the stream in some quantitative detail, as although the physical features of the different parts of the stream are shown to have marked effects upon the trout, the mode of action of these physical factors is not clear. Temperature and chemical data are more scanty but probably the very slight differences along the stream are unimportant.

The second part is devoted to the fauna other than the trout itself and is mainly a quantitative survey of the bottom fauna based on bimonthly sampling in the different zones. Estimates were made of the density in numbers, dry and wet weight of the total fauna and its principal constituents. Detailed taxonomic analysis was limited through inevitable lack of the basic knowledge, which is still incomplete even in England, let alone New Zealand. Some observations on other animals are given, of these only the eel is probably of much importance, and investigations on it are apparently still in progress.

The next part deals with the trout itself and the estimates of population, mortality, growth, food, and cropping by anglers. Population and mortality were estimated by quarterly nettings

in all the zones together with marking experiments. The egg production was estimated both from the population and fecundity of the females and from counts of redds. Growth was traced from size distribution and scale reading, and condition was also calculated. The food was analysed quantitatively from monthly samples, and data on anglers catches from a voluntary diary census.

The final main part of the paper is devoted to the production of the trout. After a clear introductory exposition of the principles of production, stock (biomass) and crop, these are then calculated, from the basic data previously described, for the different parts of the stream. An average total stock of 1100 kg. was present, and the normal annual production was estimated at 2280 kg. These are equivalent to 100–440 lb. acre and 250–750 lb. acre respectively. The food requirements for this stock and production are estimated from the experimental work of others and amount to 14,620 kg. per annum. About 65% of this was used for production, the rest for maintenance. Interesting tables and figures are given showing the changes in stock, production, food consumed and cropping through the life of a year-class. Of the production of a year-class 80–93% was removed by natural causes before cropping by anglers effectively began, and over the whole life only 0·9–6·5% of the production is cropped. The crop can be expressed as a percentage of the food consumed by the trout, when it becomes a measure of the efficiency from man's point of view of the food-chain link: food eaten by trout—trout eaten by man. This efficiency is shown to be 0·1–1·0%. No information is given on, or speculations made about, the fate of the rest of the production apart from some that must go to eels. Nor is any mention made of the annual loss of production in the form of eggs and milt, although this must be a significant proportion. The data for production, crop, food, etc., in the different zones are compared and discussed, and it is concluded that trout do exert a significant pressure on the bottom fauna, though these conclusions must remain somewhat tentative until estimates can be made of the production of the bottom fauna.

The most important section of the paper is this final synthesis of the data into the estimates of stock, production, crop and food consumed, but the earlier parts considered above contain much of general and special interest. For example it is significant that one short stream, differing little in temperature and the chemistry of its water throughout its length, should nevertheless show marked differences in growth-rate, population and production. These differences must partly be maintained because there is surprisingly little migration of the trout up and down the stream even at spawning time. Doubt is shed on some previous New Zealand scale-readings and the growth-rates derived from them by the demonstration of false checks on many of the scales from the Horokiwi. One important result is the demonstration of the effect of floods. A succession of minor and one major flood occurring towards the end of the period under investigation had severe effects upon the bottom fauna (in one zone reducing its density to but 20% of its former level) and on the population, growth, condition and production of the trout.

On the whole, this long paper is well set out, and fairly readable. It is possible that one or two sections, for example the mathematical analysis of growth, not being strictly relevant to the main theme, might have been omitted and developed in separate papers. The data are fully tabulated and with one or two exceptions adequately illustrated by the figures. The plates, though not always technically excellent, give a good picture of the stream and incidentally of the physical labour involved in such an investigation. It is inevitable that quantitative ecology of this type should involve much tabulation and statistical analysis of numerical data, and it is doubtful if the statistics could have been less prominent without severely detracting from the value of the work. One of the valuable features is, in fact, the effort made to estimate the errors involved. The least accurate of the estimates made are those of the bottom-fauna density and trout population, both of which are considered to have errors of $\pm 50\%$ to a 95% confidence.

The comparative refinements of the different techniques involved is discussed, and are of interest in relation to future work of this type. It is probable that electrical methods of fishing streams will ease the problems of sampling stream fish effectively for population and mortality estimates. Growth-rates can now be estimated with quite adequate accuracy. The early fry stages of fish still present a sampling problem, however, especially as it is becoming abundantly clear that they are ecologically one of the most important stages in the life-cycle. The bottom fauna, and again especially its younger and smaller constituents, cannot yet be sampled with adequate accuracy, and many refinements in technique and more information on sampling errors are still needed.

There is much of stimulating interest in this paper for the animal ecologist, the fishery biologist and the angler, but above all it is a demonstration that the time has come when we can

begin to draw some fairly firm lines in the picture of the mass-dynamics of at least one natural community. The author has asked Nature some pertinent questions and received some stimulating answers in reply.

E. D. LE CREN

INSECT DISTRIBUTION

C. H. Lindroth (1945–49). *Die fennoskandischen Carabidae: Eine tiergeographische Studie.* I. *Spezieller Teil.* Göteborg VetenskSamh. Handl. (B) **4**, No. 1, pp. 709 (1945). II. *Die Karten.* Ibid. No. 2, pp. 277 (1945). III. *Allgemeiner Teil: Zugleich eine biogeographische Prinzipdiskussion.* Ibid. No. 3, pp. 911 (1949).

Although this massive work is devoted primarily to the Carabidae (Coleoptera) of Fennoscandia (i.e. Norway, Sweden, Finland, the north-western corner of the U.S.S.R. and the Baltic Islands) it contains much material of interest to British ecologists. Part I contains a list of the Fennoscandian Carabid species, in which a number of topics are discussed for each species. First, the distribution of each is given, comprising a detailed account of the occurrence within the region of study together with a more general survey of the remainder of the distribution. This is followed by a study of the ecology, this section being devoted mainly to the types of habitat in which the species is to be found. Under the heading 'Biologie' information is given on the life-history with special reference to the overwintering stage. The next section 'Dynamik', deals with the species' power of dispersal. In some cases there are paragraphs on the fossil record of the species within Fennoscandia, and on systematics. Many of the data given are original, and where not, the source is made clear. The information given in Part I is supplemented by the series of excellent maps given in Part II. Each map gives the distribution in Fennoscandia of one species only, by marking by a point each locality in which the species has been found; of the 361 Carabids found in the area, 338 are given maps, most of them full page. There is a need for works of comparable scholarship in Britain covering many groups of animals, and for such studies the work of Lindroth under review could well stand as a model. Fortunately, some 250 species of the Carabidae found in Fennoscandia occur also in the British Isles, so that many of the data given by Lindroth can be applied to British needs.

The information given in Parts I and II forms the basis of Part III which has the sub-title, 'Zugleich eine biogeographische Prinzipdiskussion'. This part, like Part I, has a very comprehensive bibliography. This is the largest of the three volumes, and it is not possible in this review to comment with justice on all the topics discussed. In an interesting introduction Lindroth points out that there is a tendency in biogeographical work to avoid laboratory studies, the worker going instead straight from the field to the desk. He remarks that supernatural powers are often needed to determine limiting factors from field data alone. Lindroth's own laboratory experiments are based in the main on Herter's 'orgel' technique, whereby animals are tested in gradients of various factors. Some of the results of his experiments are difficult to analyse, but the results with members of the genus *Harpalus* are very interesting. Adults of fifteen species were tested; ten of these species by their geographical distribution might be considered calciphilous. In the experiments, however, these did not show a particular reaction towards calcium carbonate, but compared with the other five species, they showed a relatively greater positive reaction towards warmth or dryness. By field measurements, Lindroth has shown that limestone soils tend towards 'oceanic' conditions in that their temperatures tend to be less extreme than those for other soils. It is his contention that such soils favour warm-loving species because they lengthen the period of the year when the animals can be active. As Lindroth points out, although the chemical properties of limestone soils are probably of primary importance to plants, it is possible in some instances that this 'oceanic' tendency may play an important role with them also. 'Orgel' experiments using soils of different *p*H also failed to differentiate two groups among the species of *Harpalus*. However, to draw the conclusion from experiments such as these, as Lindroth does, that Carabids in the main are not limited by the calcium content or by the *p*H condition of the soil, seems unwarranted; the experiments were carried out on adult beetles, and it is possible that earlier stages may be affected by such factors. Lindroth has shown that some Carabids, e.g. *Dyschirius salinus*, show a positive reaction towards sodium chloride, and the distribution of these species parallels elegantly the progressive increase in salinity in the Baltic.

Much of Part III is concerned with the wing sizes of species, especially with those species showing wing dimorphism (in some cases, polymorphism). Lindroth examines thoroughly the

possible advantages accompanying reduction in wing-length, and concludes that isolated, restricted habitats favour non-flying forms and thus brachyptery. Flying forms, on the other hand, are favoured during periods of areal extension. During the Quarternary Period with its alternating glacial and interglacial periods, alternately restricting a species' distribution and allowing it to extend, a dimorphic species will have had an advantage. Lindroth gives much evidence from the distribution of dimorphic species to show that the macropterous, flying forms act as 'parachutists', occupying peripheral areas in advance of the non-flying forms of the same species. Lindroth has shown elsewhere that the wing-length of Carabids is controlled by genetic factors, the factor for macroptery being recessive. As fertilized females rarely fly, the peripheral populations of dimorphic species which are extending their range are almost pure homozygous recessive, i.e. long-winged. In fact, when the ranges of macropterous and brachypterous forms coincide, it is considered that the species has reached the limit of its extension. An example of a species with a peripheral predominance of the macropterous form is *Calathus mollis*. Another such species, *Bembidion grapei*, was earlier believed to have spread over Fennoscandia from the east since the last glaciation; however, the distribution of the wing forms suggests that this species has spread eastwards from Ice Age refuges on the west coast of Norway. Adult Carabids are well suited also to dispersal by water as they float high; Lindroth suggests that the most effective means of dispersal is what he terms 'anemohydrochorous', by which insects being carried by the wind alight on water and are concentrated by being cast up on shores.

The final sections of the book are given up to an examination of the history of the Fenno-scandian Carabid fauna. Several probable routes which various elements of the fauna have used in the post-glacial immigration are outlined. Some species appear to have survived the last glaciation (Würm) within Fennoscandia, in favoured areas along the Norwegian seaboard. Lindroth supplies evidence from what is known of the climatic conditions of nunataks showing that such 'overwintering' is quite feasible.

Although the text is written in German, there is a very comprehensive English summary of 29 pages to Part III; in addition all the figures in this part have both German and English legends. One section of the summary reads: 'It is a strange fact that in Great Britain—in this respect the most suitable country of Europe (Iceland perhaps excluded)—so little interest has been devoted by entomologists to biogeography. The best biogeographical survey of British Coleoptera has been made by a foreigner (Sainte-Claire Deville, 1930)!' Certainly a study of the British Carabidae paralleling the studies of Lindroth would be very interesting.

OWEN GILBERT

PHYSIOLOGICAL ECOLOGY

O. Harnisch (1951). *Hydrophysiologie der Tiere: Elemente zu ihrem Aufbau.* Pp. viii + 299; 62 text-figures. *Die Binnengewässer*, Vol. XIX. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung. Price, paper DM 49, bound DM 52.

The present statistical and genetical trend in Ecology has focused attention mainly upon populations and upon the environment as determining the size, genetic constitution and mass behaviour of populations. The revival of interest in the Theory of Evolution as well as obvious and pressing economic problems has very properly stimulated this direction of study. There remains, however, the more intimate problem of the detailed nature of the interactions of individual animals with the environment. Though most of the data of animal physiology are relevant in one way or another to this subject, they are not always considered in this context and general surveys of what might be called 'Physiological Ecology' are few.

Prof. Harnisch's 'Hydrophysiologie', being the 19th volume of the Binnengewässer series (edited by Prof. Thienemann), is a survey of some of those problems in animal physiology which are especially relevant to life in fresh waters. The principle subjects chosen for discussion are—Osmotic and Ionic Regulation; Hydrogen Ion Concentration; Reactions to Toxic Substances; Specific Gravity of Aquatic Animals; Effects of Temperature; Reactions to Light, Chemical and Mechanical Stimuli; Feeding and Nutrition.

The book was written in Germany since 1944 under conditions of extreme difficulty and with what the author admits were very inadequate facilities for consulting recent literature, and specialists in any of the subjects listed above would find some grounds for complaint on this score. Reproductive phenomena, life-cycles and related topics are not included, nor is there any discussion of the dynamics of movement in water. There has been sufficient work in both these fields to warrant their inclusion in such a book. The most authoritative as well as the

longest chapter is on Dissolved Gases and Respiration. This is of course Prof. Harnisch's own subject to which he has contributed much with his work on *Chironomus*, and there is a very interesting discussion of aerobic and anaerobic metabolism based largely on his own researches.

The laboratory physiologist must necessarily abstract from the whole and study each process separately, from which may be deduced the absolute limits to the activity of an animal in the face of a given external factor. But under natural conditions the behaviour of an animal is not always what would be predicted from a laboratory study, which is hardly surprising in view of the complicated nature of the environment. Not only are there in all probability external influences at work as yet unknown, but the reactions of an animal to one factor is usually influenced by another, and survival and distribution of a species depends upon successful interaction with the environment at all stages of the life-history. This does not mean that analytical physiology is not an essential basis for a better understanding of animals in nature, but most readers of this book will be impressed with the ultimate limitations of the traditional laboratory techniques, and by the future in store for the competent physiologist who is also a good naturalist and who will combine his analytical investigations in the laboratory with observations of animals in the field or at least under conditions as close as possible to nature.

This book should certainly stimulate an interest in the many unsolved problems in the physiology of fresh water animals and it is to be hoped that Prof. Harnisch will sometime be able to write another edition incorporating more recent work bearing upon those subjects which he discusses.

L. C. BEADLE

THE BIOLOGY OF FRESH WATERS

T. T. Macan and E. B. Worthington (1951). *Life in Lakes and Rivers.* Pp. xvi + 272; 72 plates; 20 text-figures. New Naturalist Series. London: Collins. Price 21*s*.

This is undoubtedly the best and most readable book on general fresh-water ecology that has yet been published in English, and although it is written in a manner that will appeal to amateur naturalists it will also be of great use to serious students of biology. It contains a surprising amount of information, amongst which are summaries of most of the important fresh-water biological researches that have been undertaken in this country.

Throughout the book the authors have adopted a purely ecological approach, and despite the many gaps in our knowledge they have succeeded in giving a connected and stimulating account. They open with a general discussion of the environment in lakes and rivers, and the various factors which operate on living organisms in them. For lakes they deal with such phenomena as thermal stratification and its biological consequences, the penetration of light, the cycle of plant nutrient salts, wave action and erosion, and the influence of the formation of the shoreline on the substratum in shallow water. They continue with a survey of the different kinds of lakes, their various origins and their evolution and classification. There is also an excellent account of the interpretation of the stratification of deep water deposits from Windermere, and the correlation of this interpretation with the known history of the watershed. In this section of the book a chapter is devoted to the apparatus and methods which are used in the study of lakes.

The section on rivers is less connected; inevitably so since these have been relatively neglected both in Britain and elsewhere. It consists of a brief account of the various schemes that have been advanced for the classification of water-courses, followed by a review of the various river surveys that have been made in this country, and a brief discussion of the ecological factors which appear to control stream organisms. It is surprising that no mention is made here of the extensive studies which J. R. Erichsen Jones has made on Welsh rivers and streams.

There follow three chapters dealing in greater detail with the organism and its environment. The first surveys the flora and fauna of British fresh waters, and the second continues with a discussion of the various animal and plant communities found in aquatic habitats. This leads to a survey of recent detailed work on certain organisms, or groups of organisms, which shows how measurable factors in the environment influence their distribution and occurrence. The productivity of natural waters is then discussed, with special emphasis on the extreme difficulty of finding out how much this is, and this is followed, later in the book, by a discussion of fishery biology and the increase of fish production by the manurial treatment of ponds. Thus chapters 9, 12 and 13 should be of great interest to practical fishermen, and will, one hopes, explain to them the dangers of any facile approach to the problems of obtaining more and bigger fish.

One chapter is devoted to 'life around the water', and in it the development of swamp, marsh, fen and bog are described, and the various mammals, birds and amphibia associated with aquatic environments are briefly noted. Another chapter deals with 'animal travels'; it discusses the life-histories of the eel and the salmon, and gives some account of the movements and dispersal of various invertebrates. Perhaps more could have been made of the second part of this chapter; no mention is made of the peculiar resting eggs, statoblasts, etc., which are so important in the dispersal and survival of many of the smaller organisms.

The last two chapters are concerned with the problems of pollution and water supply, both of which are very important in this country. Inevitably both accounts are far from exhaustive, but they are very welcome in that they show a biological rather than the more usual and less fruitful chemical approach. It is also refreshing to read a popular account of the problem of pollution that is reasonable and not wildly partisan.

Of the plates forty are coloured, and, as in some other books of this series, some of these are disappointing. A few are, however, quite correctly coloured and satisfactory, which indicates that it is not the reproduction that is at fault, but that the photographic editor might be more selective in passing photographs for publication. The thirty-two black and white plates are very good, but it is odd that the specimen of *Gammarus pulex* chosen for illustration should be without several of its legs, and that the *Argulus coregoni* which is clearly figured in ventral view should be described as in 'dorsal aspect'.

These are, however, small points that do not really detract from the value of the book, in which each of the various aspects of the subject have received careful and detailed treatment, to which it is impossible to do justice in a brief outline. The authors are to be heartily congratulated on producing a book which will be welcomed by many. H. B. N. HYNES

THE PARASITES OF BIRDS

Miriam Rothschild and Theresa Clay (1952). *Fleas, Flukes and Cuckoos: a Study of Bird Parasites.* Pp. xiv + 304; 40 plates; 5 text-figures. New Naturalist Special Volume. London: Collins. Price 21*s*.

This book is an account of the various groups of parasites which live in or on birds, with a discussion of other relationships in which birds are involved, such as symbiosis and commensalism. It is a study of a community of animals, plants and bacteria which, as the editors point out, is just as real as any of the communities of wood, stream, field or sea. Most naturalists who have handled birds, or their nests, will have come across parasites. If they have got over the first feeling of repulsion, they have probably wanted to know more about these parasites, but this in the past has been an impossible task for the non-specialist. A tube of fleas or lice may even have been sent to the British Museum, and a name supplied by one of the authors of this book, but the sender of the tube remained completely in the dark about the life-history and significance of his parasites. The book here under review has completely changed this state of affairs, and should stimulate a new interest in birds as carriers of parasites.

The book is divided into three parts. Part I deals with the general aspects of the subject and includes chapters on Parasitism, Commensalism, Symbiosis, Effects of Parasites on the Host, Effects on the Parasite, and the origin of Parasitism. Part II is perhaps the most exciting part of the book and gives an account of Bird Fleas and Feather Lice, to illustrate in more detail the relationship between bird host and parasite. The two authors are widely recognized authorities on these two contrasting groups, Miss Rothschild on the Aphaniptera and Miss Clay on the Mallophaga, and they have rendered a valuable service to zoology by summarizing their own knowledge and that scattered in the literature into a hundred readable pages.

The structure, life-history, habits, distribution, origin and evolution are described for each of these orders. Fleas are not particularly successful as bird parasites, only a few having succeeded in changing over from mammalian hosts, so that it has been possible in the chapter on Fleas to describe briefly all the fourteen British bird fleas, with plates illustrating specific differences in the shape of the receptaculum seminalis and of the male genitalia. The transfer from mammalian to bird hosts has taken place in comparatively recent times and in most genera of bird fleas it is possible to tell from which group of mammalian fleas they have been derived. The authors suggest that the evolutionary trends associated with this change to life in feathers present a gigantic field experiment to the naturalist who takes the opportunity of studying it. Feather Lice, on the other hand, are a very ancient and highly successful group on birds, less

so on mammals. There are about 1500 species recorded from Britain, so that their classification can only be dealt with briefly and some account given of the genera found on the various orders of birds. The evolutionary relationships between many of these bird orders have always been a puzzle to the systematist, and perhaps the greatest interest of the Mallophaga is that they have not diverged so widely as their hosts from the parent stock, due to the equable environment in which they live, and so can often provide valuable evidence about the relationships of their hosts. Examples are given and there is a frank discussion of the possible errors in interpretation, but the authors conclude that, if one order of birds harbours three or more genera of Feather Lice common to another order, then this is strong evidence of close relationship, which should be considered seriously by the ornithologists. In both these chapters, and indeed in the whole book, there is a refreshing admission of the lack of knowledge and the great need for more collecting and more ecological observations.

Part III presents a more rapid survey of all the other groups of parasites which attack birds in Britain. There are chapters on Protozoa, Vermes, Flies, Mites and Microparasites, each containing much information of interest to zoologists, which they could not easily find elsewhere, and providing a useful summary of what is known of these groups as they affect birds. There follows a fascinating chapter on the Fauna of Bird's Nests, which concludes with the sound advice for bird lovers to remove old nests from nest boxes and buildings, before the following breeding season, so reducing the hours of misery, pain and disease for future nestlings. Finally there are short chapters on Skuas as cleptoparasites, and the Cuckoo as a brood parasite.

The illustrations consist of forty black-and-white photographs, and a number of line drawings by Arthur Smith, which are both decorative and informative. The photographs are good half-tone reproductions which to many people will seem very much better either than the indifferent colour plates or the photogravure reproductions in most of the New Naturalist books. Many of these are photomicrographs, which add materially to the value of the book, but the remainder are mainly photographs of birds, excellent in themselves though often contributing nothing to the text. Surely the swan and the robin, for example, can be visualized without a photograph by anyone likely to read this book, whereas a few more photographs of parasites would have been much more relevant. There are five text-figures, but unfortunately no index to them, and a useful bibliographical appendix, arranged chapter by chapter, which provides suggested literature for those wishing to study the subject further.

But for the New Naturalist publications this book would probably never have been written, at any rate in its present admirable form; it is both readable and stimulating for the general naturalist, and a valuable summary and source of information for the zoologist. Parasites as a subject may not appeal to a wide public, and it is to be hoped that the sales of this volume will not discourage the publishers from issuing further special volumes of this quality, which open the eyes of so many people to communities of which they were previously not even aware.

P. F. HOLMES

ELEMENTARY ECOLOGY

W. H. Dowdeswell (1952). *Animal Ecology.* Pp. xvi + 207; 16 plates; 45 text-figures. London: Methuen. Price 12*s.* 6*d.*

The growth of 'Scientific Natural History' has been accompanied by a flood of researches and publications by innumerable workers on a front so broad that the beginner finds the subject ill-defined and hazy. In plant ecology the groundwork has been well covered, in recent years, in a number of text-books in which the fundamental concepts of this discipline are stated and defined. The factors operating on plant communities are relatively easy to enumerate and measure; seasonal and seral changes are often distinct if not spectacular, and identification of material is comparatively easy.

The situation for the animal ecologist is unfortunately less happy. His material seems more refractory; the identification of his specimens is often difficult or the work of a specialist; ecological relationships seem obscure, and numerical fluctuations are discernible only on a subjective basis or after laborious sampling and statistical treatment. If a royal road through these difficulties (which have their fascination and value as stimulants of endeavour) were available, there would still be a need for a simple statement of the principles of Animal Ecology and their application. This is what the author of this small introduction has endeavoured to provide, and though it is regrettable that the size of the book has been so rigorously curtailed, he achieves a considerable measure of success.

The arrangement is simple and direct. An introductory chapter gives the historical and geological background of ecology, and includes a short history of the British fauna. A chapter on the distribution of animals deals all too summarily with the cline concept, adaptability, isolation and kindred topics. Some other fundamental issues such as food relationships and food chains, simple population concepts, dispersal and migration make up a useful third chapter. Examples to illustrate the author's points are well chosen and up to date. Next come the parasites, commensals and symbionts, a useful though somewhat elementary chapter, oddly omitting reference to inquilines. Four chapters deal succinctly with the environmental features of land, marine, estuarine and fresh-water habitats, and in a final chapter of practical suggestions, some useful hints are given together with constructional details of some easily made bits of simple apparatus. There is a short but excellent section on the statistical treatment of samples which ought to encourage the least mathematically minded student to accord his results the simple but often neglected treatment which so enormously enhances their value.

The seven-page bibliography is conveniently arranged and forms a fairly complete list of standard works. No original papers are referred to, but the list will prove helpful and suggestive to elementary students and to school librarians. Such a list could not be exhaustive, but it seems curious that the 'Genetics' of Darlington and Mather should be included but not that of Waddington; the Ray Society monographs (such as Locket and Millidge's Spiders) are not referred to in the section devoted to key works for identification, nor are the limnological text-books of Welch. More unaccountable omissions are the pamphlets of the Linnean Society and the Freshwater Biological Association. Difficulties of identification would be greatly reduced if more specialists could be prevailed upon to publish small and inexpensively produced pamphlets dealing with their particular groups, and every such effort ought in the reviewer's opinion to receive the widest possible publicity. It is scarcely possible to undertake or direct any venture in animal ecology without running into this difficulty of identification; no doubt more than one reader will recall suggestions that dustbins, rubbish heaps and gutters can form valuable ecological training grounds for the less fortunately situated, and perhaps even the collections of Collembola, rotifers or earthworms which resulted—and remain unidentified.

The book is well produced and adequately illustrated, though some of the blocks are old friends and at least one (Saville-Kent's *Carchesium*) is highly unlifelike and ought to have been improved upon. It is surprising to find no reference to the animal inhabitants of soil, nor indeed to the existence of soil as a habitat. Fertilization of 'winter eggs' of Cladocera occurs before the ephippia are shed and not in the following spring as stated (p. 138). More might be made, even in a book of this size, of the behaviour of relict planarians than the bare statement that they show negative thermotaxis.

Some of these grounds for criticism are clearly the result of the rigid limits which have been imposed on the size of the book. A great deal of information has been clearly, attractively and suggestively presented within these limits, and the book deserves commendation as a courageous and largely successful attempt. P. H. F. WHITE

BOOKS RECEIVED

Animals as Friends. By MARGARET SHAW AND J. FISHER. (New revised edition.) London: Dent. 1952. Price 15*s.*

Furred Animals of Australia. By ELLIS TROUGHTON. (Fourth revised edition.) Sydney and London: Angus and Robertson. 1951. Price 35*s.*

N.A.A.S. Quarterly Review, No. 15, spring 1952. London: H.M.S.O. 1952. Price 1*s.* 6*d.*

The Times Agricultural Review, No. 1. London: The Times Publishing Co. June 1952. Price 6*d.*

ABSTRACTS

EDITORIAL NOTE

In Volume 22 it is hoped to resume the series of abstracts which appeared under the title 'Notices of publications on the animal ecology of the British Isles' in each number of the *Journal* up to Vol. 20, No. 2. The editing of the new series has been undertaken by Prof. L. A. Harvey with the voluntary assistance of R. Bainbridge, H. F. Barnes, G. I. Crawford, A. E. Ellis, R. S. R. Fitter, I. M. Goodbody, A. Macfadyen, C. Matheson, E. Nelmes, E. R. Parrinder and Miss G. Watt. Like the old one the new series will aim at covering all the significant publications in British journals and reports dealing with the ecology of the British fauna. A special effort is being organized by Mr R. S. R. Fitter to cover the publications of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by regularly sending copies of their publications to R. S. R. Fitter, Esq., Greyhounds, Burford, Oxford. Others can also assist by sending re-prints of their papers or offers of help in making abstracts to Prof. L. A. Harvey, University College, Exeter.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING

3–4 April 1951

A general paper-reading meeting was held in the rooms of the Linnean Society, London, on 3–4 April. The President, Dr W. B. Turrill, was in the chair.

Miss Ruth Badcock opened the morning session on 3 April with her paper on the ecology of the Hydropsychideae (Tricoptera), based on her work in parts of Scotland and Wales. Dense populations of *Hydropsyche* are associated with lake outflows, and are absent from inflows where the water is soft (e.g. Ca^{11} less than 10 mg./l. and often only 2–3 mg./l.). In streams the necessary nutrient conditions are only found where water is hard. The larvae with their fixed shelters can withstand swift currents, but they are usually protected from them by being in sheltered microhabitats (under stones or in moss). The swift current acts mainly by its influence on the substratum in preventing stagnation.

Warm summer temperatures are necessary (in Britain maximum temperatures in excess of 15° C.) and the higher summer temperatures of lakes may be an important factor, though the most significant effect may be to increase the planktonic food supply. The larvae catch plankton in a net, browse on the algae of the stream-bed and eat small nymphs' larvae. The ecology of individual complex populations of *Hydropsyche* larvae has yet to be elucidated. *Diplectrona felix* has a distinct habitat in small stony trickles.

Miss Badcock also considered the possible methods of the selection of streams by female imagines.

Prof. G. C. Varley, Dr Le Cren, Prof. J. B. Cragg and Dr R. E. Hughes took part in an interesting discussion, which had particular reference to the ultimate effect of nitrogen supplies on nutrient conditions.

Mr D. S. Johnson followed with a paper on the localization of *Cladocera* in lakes and ponds. The *Cladocera* fauna of different lakes and ponds is not easily related to environmental conditions, but those of different habitats within a lake are often distinctive. Forms of the littoral weed-bed and of the lake bottom were mainly discussed, these falling into two groups, detrital and algal feeders. Food preferences strongly determine the occurrence of certain species. In the case of the bottom feeders, the size of particles on the bottom itself is important, different species occupying rock or stone, sand and mud, while others are buried in debris, or burrow in thick vegetable deposits.

The reaction to aquatic plants is less apparent. In the case of *Chydorus sphaericus* there is a real association with higher algae. The mechanical effect of wave action and exposure on the littoral fauna is important, but difficult to separate from other factors. The 'littoral avoidance' theory was considered to be unsound as plankton may occur in littoral sheltered weed-free areas. The actual distribution is however very complex owing to the interaction of various factors. Localized swarms may occur, probably due to varying narrow zones of optimum conditions.

A discussion followed, particularly on the possible mechanical effect of wave action on the distribution of *Cladocera*. Dr W. B. Turrill, Dr Le Cren, Profs. T. G. B. Osborne, J. B. Cragg and G. C. Varley took part.

R. S. Fitter read a paper on towns as habitats for animals, discussing in particular factors such as variation in tolerance to man and functional preferences in choice of micro-habitat. The relationship between the natural habitat preferences of a particular animal and the choice of alternative ones in towns was an important aspect of the paper.

C. Burton, A. D. Middleton, G. C. Varley took part in the discussion that followed.

The work of the Nature Conservancy was described by Captain C. Diver. He stressed the great importance of research in working out satisfactory methods of reserve management. This kind of activity could be provided for by the work of post-graduate students, by research grants to Universities and similar institutions, and by the proposed two research stations of the Conservancy. The first step would be the management of the vegetation, while work on distributional surveys, autecology of species (in particular range of tolerance to habitat factors) was important.

Prof. J. B. Cragg, Dr M. E. Solomon, Dr A. D. Middleton, Profs. A. D. Peacock and G. C. Varley took part in the discussion that followed.

The afternoon session was commenced by a very stimulating paper by Dr C. B. Williams, in which he discussed an attempt to measure changes in a mixed insect population under natural conditions in the field, and to see to what extent they are quantitatively related to previous weather conditions.

To obtain a measure of the population, insects were caught in a light-trap at Harpenden, about 25 miles north of London, every night for 4 years from 1933 to 1937, and again for 4 years from 1946 to 1950. In all about 1,440,000 insects, mostly Diptera, were captured on about 2850 nights.

It was shown that a very high proportion of the mean changes of the population in the field can be accounted for by the effect of rainfall and minimum temperature in the three previous months.

An examination of the regressions in the different seasons shows that rainfall has a high positive effect in the summer and autumn but little or no effect in the winter. Minimum temperature, on the contrary, has its lowest effect in the summer, so that the relation between population and minimum temperature 1 month previous is negative in the summer, and with temperature 2 months previous is negative in the autumn.

The analysis of the available data has so far only been carried out on the total insect population, against rainfall and minimum temperature. Work is continuing on other weather factors, other time intervals, and also on special groups of insects, but it is unlikely that the method will be applied with any great accuracy in the near future to single species of insects.

This paper suggested a much wider field of application both in plant and animal ecology. This was amply borne out by the discussion that followed, in which Prof. Varley, Captain Diver, Miss Macleod, Miss Warkoff and Dr Fraser-Darling took part.

Dr M. E. Solomon followed with an account of the ecology of pests of storage products. Slides were shown of pests, foods, and mode of storage. He dealt with the rates of population increase of the insects concerned, showing how laboratory experiments gave an indication of the maximum rates of increase. Under actual conditions of storage these rates are not attained due to unfavourable conditions and raised population density. At low densities there is a simple linear relationship between density effect and density, but at higher levels (insects per gram) there is often an exponential relationship. No further increase in population occurs when there are greater than 10–15 adults/g. An interesting result was that there appeared to be an optimum density for population growth (varying between 0·1 and 5 adults/g.), too low densities being unfavourable. In storage products population density often does not reach a level at which density effects set in, except at favourable points or near the site of initial infestation. In this study of rate of increase and maximum density a number of factors must be taken into account, in addition to density effects, such as physical conditions, cannibalism, competition, disease, predators and parasites. The time interval involved before treatment or removal of the storage product is obviously important. In the discussion that followed, Dr C. B. Williams, Prof. J. B. Cragg, Dr O. W. Richards and Miss Macleod took part.

Dr D. W. Morley was unable to give his paper on extraordinary and ordinary ants' nests.

On the evening of 3 April a soirée was held in the Herbarium of the Royal Botanic Gardens, Kew, by kind invitation of the Director, Sir E. J. Salisbury. A very pleasant evening was spent, as the staff at Kew had provided excellent refreshments and a wide range of well-set-out exhibits.

These exhibits include recent ecological publications from Kew, modern european floras, photographs of Chinese vegetation by the late G. H. Wilson, various vegetation maps, manuscript maps illustrating parts of East Australia, drawn by the late explorer, A. Cunningham, soil preferences of British species or *Carex* etc. Two lecturettes were also given by (1) F. Ballard on a Botanical Expedition to Ceylon, (2) P. R. O. Bally on the East African vegetation and fauna. Both of these were excellently illustrated by natural colour slides.

Prof. Varley terminating the evening meeting thanked the Director and his colleagues for the excellent arrangements which had been made.

4 April. The first paper was that of G. W. Dimbleby who read a stimulating and controversial paper on the history of the Hackness of the Tabular Hills, Yorkshire. This area is of interest ecologically and pedalogically, as it is said to be unglaciated. Dr Dimbleby described a new technique of the pollen analysis of mineral soil, showing how pollen of late-glacial elements can be found in soils. The washing

down of pollen destroys any stratigraphal significance of the results, but certain species are indicative of certain post-glacial periods and broad vegetational types. It was concluded that not only the Hackness outlier but the whole of the Cleveland massif bore hardwood forest in atlantic times. The disappearance of forest coincided with the bronze-age occupation, subsequent fluctuations of population probably allowing temporary reversion to forest in some areas. But the trend to the development of moorland progressed relentlessly. It was estimated that the Hackness moors as known to-day, date back to the Middle Ages or earlier. Podsolic soils developed from the brown earths of the old hardwood forest, probably matured at about the same time. In the discussion that followed Drs W. B. Turrill, M. E. Solomon and R. E. Hughes took part.

Dr D. E. Coombe then showed a series of slides illustrating the habitats of some of the rarer plants for which the Lizard Peninsula in Cornwall is noted. His paper was largely concerned with the factors determining the occurrence of these species. They are found primarily on south-facing slopes where summer insolation is high, in a plant community in which herbs are prominent with a few grasses like *Festuca ovina*, *Koeleria gracilis*, and a number of annuals. On north slopes the rare species are absent, and the community is a close turf of the common pasture grasses. Apart from insolation, the present abundance of *Trifolium molinerii*, *T. strictum* and *Herniaria ciliata*, is determined by man's restriction of heath and scrub development in the grazing areas, though there are habitats present in which in the absence of grazing they would survive. Similarly, *Juncus mutabilis* (*J. pygmaeus*) occurs in open disturbed habitats, e.g. cart tracks, field entrances and an old serpentine pit. Only on the Goonhilly Downs has it been found in an undisturbed site in heath. Other species discussed by Dr Coombe were *Isoetes hystrix*, *Trifolium bocconi* and *Juncus capitatus*. In the discussion that followed the factors, particularly grazing, that determine the occurrence of these species were dealt with. Those taking part were Prof. Varley, Dr Turrill, Dr R. E. Hughes and Dr A. S. Thomas.

Mr P. Greig-Smith read a paper on secondary forest in Trinidad, B.W.I. The paper was of considerable interest, in that it illustrated the application of statistical methods to the study of succession, and interplant relationships within specific communities, at different subseral stages.

The tree and shrub vegetation of five samples of forest in Trinidad, B.W.I., was examined in detail, using a lattice of 5 ft. square plots. One represented comparatively undisturbed forest, two degraded forest and two stages in succession of secondary forest, mesophyll species being generally prevalent. Survival rates at the lower height classes were greater at the disturbed sites, and at the larger height classes greater at the undisturbed sites. The floristic composition showed a smaller proportion of individuals of endemic species at all the disturbed sites, and a higher proportion of species of wide geographical distribution and of drier forest types at the secondary forest sites. Leguminosae and Myrtaceae decreasing and Rubiaceae increasing in importance with disturbance. Species mostly showed a random arrangement of individuals at the undisturbed site, and it was suggested that early colonization is random and later colonization by spread from random pioneer individuals, resulting in heterogeneity on an increasing scale, or for species for which the environment is marginal, non-random colonization determined by small environmental differences. The association between species at the undisturbed site corresponded to chance expectation. The early stage of secondary forest showed some interdependence between species, the later stage considerably more, some pairs of species showing greater association than expected, others less. It is not clear whether this represents true interaction between species or is a reflexion of environmental differences.

A stimulating and critical discussion followed in which Dr E. W. Jones, Prof. Champion, Dr A. S. Thomas, and Dr J. Hope-Simpson took part.

The morning session concluded with a paper by Dr E. W. Jones on the history of a Nigerian rain forest. During the winter of 1947–8 the Cambridge Botanical Expedition to Nigeria made a close study of a square mile of forest in the least disturbed part of the Okomu Forest Reserve, 28 miles from Benin. From the study of charcoal (mainly oil palm kernels) and pottery at depths of 10–12 in. in soil and from apparently man-made burrows of an indefinite remote date, it was concluded that the area now densely wooded, was once intensely farmed. Various explanations were suggested for the depopulation, such as, the slave trade, disease (smallpox and tsetse-fly), wars and rebellions between the seventh and nineteenth centuries. The large emergent trees of the area are about 150–200 years old, and it can be concluded that the present forest grew up in the latter part of the eighteenth century. An interesting contrast was made

with the forests of the Cameroons. There little former disturbance with woodland has occurred, the forests are far poorer in emergent large trees of economically valuable species. The discussion that followed dealt primarily with the present status of tropical forests, Dr A. S. Thomas, Prof. Champion and Dr Hope-Simpson taking part.

In the afternoon Dr J. D. Ovington discussed some ecological problems of afforestation. Less than 5 % of the British Isles are forest covered. The Forestry Commissioners require 3,000,000 acres of new woodlands. The limited sites available for afforestation cover a range of ecological types, many of which have been eroded and impoverished since the early forests were felled. The selection of the most suitable tree species for any particular site is most important and the forester should consider (1) the expected growth performance, (2) the preparatory treatment for aiding the establishment of plantations, and (3) the effects of afforestation upon the site and ultimately the succeeding crop.

The recognition of plant communities and the distribution of indicator plants help to assess the sylvicultural possibilities of a site, but recent forest research has demonstrated that sites can be modified by such treatments as screefing, ploughing, etc., so as to establish more exacting species. The effect of afforestation upon (1) the development of a leached A_2 horizon, (2) the accumulation of litter, (3) the biological activity of the soil, (4) soil acidity and buffer capacity, (5) nutrient status of the soil, (6) physical conditions of the soil, (7) the micro-climate, (8) soil-plant water relations and (9) ground flora, were discussed.

It was suggested that the forester can, by suitable choice of species and forestry management, influence the direction and rate of change of ecological conditions following afforestation so that site quality is conserved and where possible improved.

Mr A. Brownlee, Agricultural Research Council Field Station, Compton, then made an analysis of the instincts of skin-hygiene, curiosity and play as they are manifested in domestic cattle. He divided these instincts into component parts of drive, releasers, emotion, conation, and goal, and pointed out the factors inhibitory to the drive in each case.

In the discussion that followed Mr Watkins took part.

The meeting terminated with a account by Dr William Davies of the aims and methods of the survey of European grasslands at present being sponsored by the Organization for European Economic Co-operation. The grassland survey of England and Wales, conducted by Sir George Stapledon, Dr Davies and their colleagues, was discussed in some detail. Their survey and subsequent developments can be subdivided into three: (1) reconnaissance of grassland types so as to define the major grassland zones, (2) the detailed study of each zone to determine the proportion of contrasting pasture types, and (3) grassland experimental work to determine the relative potentialities for improvement of the different zones.

Since grasslands are of major importance in food production, the O.E.E.C. has fostered the initiation of similar surveys and subsequent developments in continental Europe. Thus with this end in view, during 3 months of the early summer of 1951 a team consisting of two Americans, one Australian, one South African, and two British has conducted a reconnaissance of the Mediterranean region.

An active and controversial discussion followed, which dealt primarily with the feasibility of an effective survey in 3 months, and also the difficulties that might arise due to different systems of grassland classification used by various countries. Those who took part in the discussion were W. B. Turrill, C. E. Hubbard and R. E. Hughes.

The President concluded the meeting by thanking the Linnean Society for the use of their rooms, and the Secretaries for organizing the meeting.

SUMMER MEETING IN NORFOLK

6–13 July 1951

The 1951 Summer Meeting was held in Norfolk and was attended by 66 members, of whom 47 stayed for five or more days. The Society was accommodated at the ex-Training College at Morley, about 12 miles from Norwich, which had recently been taken over by the Norfolk Education Committee to provide accommodation for summer courses, etc. From this base, daily expeditions were made by coach to various parts of the county.

On the evening of its arrival in Norfolk, the Society was entertained by the Norfolk and Norwich Naturalists' Society at a soirée held in the Norwich Castle Museum. Here, members were able to see the large-scale dioramas of typical Norfolk habitats, which are a well-known feature of the Museum. An exhibition, entitled 'Norfolk Naturalists at Work', which had been erected a fortnight earlier in connexion with local Festival of Britain activities, was also on display. Among others, this included panels relating to Nature Reserves owned by the Norfolk Naturalists' Trust, the biological basis of the East Anglian herring industry, and the physiography and vegetation of the Norfolk Broadland. Living material exhibited included an extensive collection of Norfolk sedges and marsh orchids.

Several members of the Norfolk and Norwich Naturalists' Society subsequently joined the British Ecological Society on excursions during the week.

Saturday, 7 July

Surlingham, Rockland and Wheatfen Broads (Yare Valley)

Leaders: Dr J. M. Lambert, Mr E. A. Ellis and Prof. A. R. Clapham, assisted by Mr A. C. Jermy.

Members first travelled by coach to Surlingham Ferry, then boarded a privately chartered river launch to carry them downstream past Surlingham Broad to the Wheatfen area. The launch made two stops along the river to enable the party to disembark and examine features of especial interest in the adjacent fenland. At the first point, two typical Broadland 'pulk-holes', surrounded partly by carr and partly by tussocks of *Carex paniculata*, were demonstrated. The pulk-holes are small residual pools, of at least semi-permanent nature, left behind as relicts in the growing up of larger sheets of water, and characterized by the absence of an encroaching reedswamp fringe (*J. Ecol.* **39**, 1951, p. 167). The second stop was made at the Bargate Nature Reserve, recently acquired by the Norfolk Naturalists' Trust. It comprises an area of formerly drained alluvium, chiefly peat, which became derelict about 40 years ago and has now reverted entirely to fen; most of its present pattern of plant communities can be directly related to the access of tidal (non-saline) water through the broken and pervious embankments which surround the area (*Trans. Norfolk & Norw. Nat. Soc.* **17**, 1951, pp. 123–35). A good view of Surlingham Broad, which was too shallow to be entered by the launch, was obtained from the Bargate embankment, and its characteristic floating marginal reedswamp of *Glyceria maxima* hover was very evident (*J. Ecol.* **33**, 1946, pp. 230–67).

The party finally left the launch about a mile farther downstream, and walked (or rather, scrambled) through rough fen and carr to Wheatfen, where a halt was made for lunch. In the afternoon, members split into small groups under the different leaders to examine communities characteristic of the Yare valley fenland around Rockland and Wheatfen Broads, while some took advantage of small punts, kindly lent by Mr Ellis, to make a tour of the waterways under the guidance of a local marshman. The areas visited by different sections of the party included primary *Glyceria maxima* and *Phragmites communis* fen, as well as former mowing marsh with a patchwork of dominants and a rich subsidiary flora (*Trans. Norfolk & Norw. Nat. Soc.* **13**, 1933–4, pp. 422–51).

Tea was provided at Wheatfen through the kindness of Mr and Mrs Ellis, and the party returned to Wymondham about 7 p.m.

Sunday, 8 July

Scolt Head Island

Leaders: Prof. J. A. Steers, Dr A. S. Watt and Mr E. A. Ellis, assisted by Mr D. Poore.

The party travelled to Brancaster Staithe by coach, and were thence conveyed to the island by boat. In the morning, the general physiography of the area was described by Prof. Steers, using the high dunes near the Hut as a viewpoint from which the general structure of the island could be demonstrated. The long and relatively new West Arm has several lateral ridges on its landward side. These ridges separate areas of marsh, and the stage of development of the marshes can be very well seen. Those nearest the Far Point are still virtually sand flats, whilst nearer the Long Hills the amount of saltmarsh vegetation increases. In the very much enclosed Anchor Marsh the marsh has developed to quite an advanced stage, whereas in about 1920 it was quite bare. East of the Long Hills the marshes are much more developed. Missel Marsh, south of Butchers Beach, shows extremely well the development of *Salicornia*, *Suaeda maritima* and *Aster tripolium*. It also shows the development of creeks very well in the vegetated part

and demonstrates clearly that the creeks are due to the growth of the marsh enclosing them. On the other hand, on the higher part of the area there is still a good deal of almost bare sand and mud. The water from this drains into the creeks lower down, and so lengthens them by headward erosion. Hut Marsh, north of Butchers Beach, is much older and shows very good creeks and pans. On this marsh, sand was put down in 1935 and it is now covered by up to 10 cm. of sediment. Marshes continue to increase in age and height eastwards to Burnham Harbour, where there is an *Aster* marsh.

An important characteristic of Scolt Head Island is the long lateral ridges between the Long Hills and Aster Marsh. They extend far back from the main ridge right down to Norton Creek, and for the most part the marshes within are narrow-mouthed.

The amount of shingle at Scolt is considerably less than at Blakeney, and this is especially the case on the main beach, which is wide and sandy; along the coast of the island perhaps 200 yards of sand may be exposed at low water. The shingle rests at the head of the beach, and throughout nearly the whole length of the island is covered by continuous dunes; these reach their main development near the hut, in the middle of House Hills, and at the east end in Norton Hills. Between these three groups the main ridge is much lower, and a few years ago a break occurred at the west end of Norton Hills. In a general way, the sand hills west of Scolt Head itself show white dunes, whereas the major dune areas are typically grey dunes. Both on the Long Hills and on Scolt itself some blow-outs have been replanted with marram grass which has held them fairly well. The whole north face of the island is still receding, and recent mapping has shown a considerable and continuous recession as compared with maps made before the war. Prof. Steers emphasized that it was important to realize that the island is merely one incident in the whole of the Norfolk Marshland coast.

In the afternoon, the party split up into three main groups under different leaders for more detailed examination of the vegetation and fauna, while other members used the opportunity to make individual studies. The party was reunited for tea before the homeward journey.

Monday, 9 July

Ranworth and Upton Broads (Bure Valley)

Leader: Dr J. M. Lambert, assisted by Mr L. C. Frost and Mr A. C. Jermy.

Ranworth and Upton Broads, in the Bure valley, were visited to provide comparisons with the Yare valley broads seen 2 days earlier. Ranworth Broad is set well back from the river, but is in open connexion with it by a wide artificial dyke which allows some degree of water circulation with the diurnal tidal rise and fall of the river; this circulation is, however, much less than that in the Yare broads, which have a much greater vertical tidal range. In contrast to Ranworth Broad, Upton Broad is completely land-locked, with very little water movement within it. Whereas Ranworth possesses in its different parts examples of most of the plant communities characteristic of the Bure valley broads and fenland as a whole, the vegetation at Upton is more restricted in its composition and character (*J. Ecol.* **39**, 1951, pp. 168–9).

The two broads—Ranworth in the morning and Upton in the afternoon—were visited by some 58 members. At Ranworth, attention was concentrated on the private Inner Broad, the property of the Norfolk Naturalists' Trust. On arrival, the party was split into two groups, one of which made a tour of the carr and woodland surrounding the broad under the guidance of a local marshman, while the rest of the members rowed over the broad in small boats to look at the marginal communities; the parties changed over halfway through the morning. It was thus possible to show all members typical example, of *Typha angustifolia* reedswamp, primary *Phragmites* fen, *Carex paniculata* tussock-fen, *Cladium* fen young developing alder swamp carr, young and old semi-swamp carr, and mature mixed fen carr. Incipient pulk-holes were also demonstrated for comparison with the fully formed pulk-holes seen earlier in the Yare valley.

The two groups of members reunited for lunch at Ranworth Staithe, by the side of the public Outer Broad. In the afternoon, the party proceeded to Upton Broad where its characteristic primary *Cladium* fen was examined at length. Three small boats were available for the study of aquatic vegetation and fauna, and were used to ferry members across to the north side of the broad to an area of fen occupying the site of a former peat cutting. Here, *Cladium* was still dominant, but *Schoenus nigricans* became co-dominant in parts, with *Phragmites* also frequent throughout; much shrubby *Myrica* and *Salix repens*

also occurred, with occasional patches of colonizing birch saplings. The line followed by the party at Upton Broad was roughly that of the transect and profile figured and described in *J. Ecol.* **39**, 1951, pp. 143–6, so that it was possible to relate the present vegetation directly to the underlying deposits during the course of the afternoon's visit.

Tuesday, 10 July

Blakeney Point

Leaders: Dr E. Gorham, Mr P. J. Syrett, Mr H. J. Howard and Mr W. E. Eales.

After arrival in the morning at Morston Quay by coach, and thence at the Point by boat, the party went first to the top of the main dune ridge, from which the general physiography of the Point could be clearly seen, as at Scolt Head. A visit was then paid to the field laboratory, where some of the records of work being carried out by Dr Gorham and students from the Botany Department of University College, London, were on view. Levelled transects across the dune ridges and salt marshes, together with quadrat records of the main vegetation types and some soil data, illustrated the relation between plant succession and dune and saltmarsh stabilization. Also shown were some quantitative data on the frequency of *Ammophila* flowering in different parts of the dune system, which demonstrated that flowering occurs chiefly on the embryo dunes, but also around blow-outs on the stabilized dunes. Some preliminary studies of the morphology of *Carex arenaria* rhizomes indicated that the length of rhizome between successive aerial shoots varies in a cyclical manner, and it was suggested that the annual seasonal cycle is responsible for this variation.

After leaving the laboratory, the party proceeded to the ternery at the Far Point, under the guidance of Mr Eales, the official bird-watcher.

Following lunch, the more ornithologically minded members, accompanied by Mr Eales and Mr Howard, separated from the main party, while the latter, led by Dr Gorham and Mr Syrett, visited the main types of plant community on the Point. The dune succession was examined first, starting with the embryo *Agropyron junceiforme* dunes and proceeding through the main *Ammophila* dunes to *Carex arenaria* and lichen heaths. The party then walked along the 'Yankee' shingle bank, where the recolonization of shingle after the wind-removal of dune sand was observed. Further along this bank, the transverse zonation of the vegetation was clearly evident. The bank is fringed with dense *Suaeda fruticosa*, while further up a more open community containing many species is found, *Silene maritima*, *Sedum acre* and *Honckenya peploides* being among the most abundant.

The party then went out on to the salt marshes on either side of the 'Yankee' bank. A few members ventured down to the mud flats being colonized by *Spartina townsendii* and *Zostera*, but most others examined the upper marshes dominated by *Salicornia* and *Aster tripolium*. These contain the free form of *Pelvetia canaliculata* in the pans. The only place where the attached form is found in abundance is a small stretch of exposed shingle near the mouth of one of the main drainage channels. The attached form fruits plentifully, but the free form in the pans is apparently sterile.

The soil profile of the upper part of the marsh was also demonstrated. This showed alternate bands of silt and sand, probably due to recurrent covering of the salt-marsh surface by sand blown from the dune system. The silt bands are strongly reducing, while the upper sandy areas appear to be well aerated and show a rusty staining due to ferric compounds.

The various groups of members eventually returned to the Old Lifeboat House, on the main dune system, for tea, where they met the University College students who were temporarily 'resident' on the Point at the time.

Wednesday, 12 July

Leader: Dr A. S. Watt. *Breckland*

On the eve of this excursion, Dr Watt gave a general talk to members sketching in the historical and edaphic background against which the existing mosaic of plant communities can be interpreted.

The pollen record (*J. Ecol.* **39**, 1951, pp. 285–307) shows that the countryside was wooded in Mesolithic times, and that forest clearance, begun in Neolithic times, made the ground available for the cultivation of the soil and the production of agricultural crops. The process of clearance continued until, by Domesday,

only two small woods appeared to be worth record. Writers in the seventeenth century record both in general terms and in detail the progress of soil erosion which accounts for the widespread but relatively thin blanket of blown sand and the localized thicker deposits in sand dunes. Not until the planting of shelter belts, boundary rows of pines and hedges, encouraged by an enlightened, recently established Board of Agriculture, did the soil of the area become relatively stable and the aspect sufficiently changed as no longer to merit description as a 'miniature Sahara'. To-day, large areas are covered by conifer plantations; much of the remainder, formerly cultivated on a 'shifting cultivation' principle, is now being continuously cropped with the aid of lucerne. Breckland, in short, is subjected to an agricultural and sylvicultural regime which within a generation has transformed the countryside, with effects on the human, animal and plant population which provide ecological material of great interest and importance.

The soil mosaic can be interpreted in terms of stages in the development of a soil profile from a highly calcareous soil to a mature podsol: and of profile truncation and burial by blown sand. To the numerous varieties of soil provided the vegetation is very sensitive.

On the excursion, which took the form of a round tour by coach, with frequent halts, only some of the features touched on could be demonstrated. The party visited a grazed grassland on calcareous soil and saw the chalky boulder clay differentiated to form ridges running down a gentle slope; differential leaching showed in the vegetation. Tuddenham Heath was next visited: a podsol profile and the cycle of phases in an unburned *Callunetum* were demonstrated. As also the futility of ploughing such land to yield rye 6 in. high!

A grassland, ungrazed for 40 years, provided a rich community in striking contrast to the grassland on the same type of soil but closely grazed by rabbits.

Finally, through the courtesy of the Forestry Commission, a visit was paid to the even-aged pine plantations, at Wangford, where some indications were given of the problems presented by such crops, and to the uneven-aged and naturally regenerating woods in Brandon Park.

Thursday, 12 July

Morning: Barton Broad (Ant valley)

Leaders: Dr J. M. Lambert and Mr E. A. Ellis, assisted by Mr L. C. Frost and Mr A. C. Jermy.

A brief description of the chief physiographical and vegetational features of Barton Broad was given by Dr Lambert on the evening previous to the excursion. Geographically, Barton Broad is exceptional in character in that, although it is situated in a main river valley, the river runs into and out of it instead of passing to one side, as is the case in typical main valley broads. It has been shown by Mr J. N. Jennings, however, that the situation here is due to past artificial diversion of the main river to run through the broad; the former bed of the Ant, now completely overgrown, has been found by boring in the marshes east of the broad (R.G.S. Research Memoir No. 2, 1952). Vegetationally, Barton Broad and its surrounding fenland bear a similar range of communities to those of the Bure valley broads, though an especial interest lies in the presence of small hummocks of some of the less acidophilous species of *Sphagnum* in certain areas of the primary fen. *Sphagna* appear to be completely absent round the Bure and Yare valley broads subject to an appreciable tidal rise and fall, with concomitant periodic flooding by alkaline water; their presence at Barton is probably related to the almost non-tidal nature of the water here due to the position of the broad well up a tributary valley.

On arrival at Barton Turf Staithe, the party split up into two sections. One group first visited Heron's Carr, an exceptionally fine belt of typical swamp and semi-swamp carr over lake muds, with interdigitations of fen carr over tongues of solid marginal peat; one of the chief attractions here was the presence of numerous fine plants of *Osmunda regalis* within the carr. The other group of members rowed down the length of the broad to join the rest at Heron's Carr, and visited marginal reedswamp and fen communities en route. The fine *Scirpus lacustris* reedswamps characteristic of the broad were much in evidence, with abundant patches of *Nymphaea alba* between them; the '*bolder*' (the local name for *Scirpus*) is still occasionally cut by hand for use in the manufacture of rush mats, though the practice has declined very much during the last 20 or 30 years due to increasing labour costs. The primary fens bordering parts of Heron's Carr yielded three species of *Sphagnum*—*S. squarrosum*, *S. recurvum* and *S. fimbriatum*; another

feature of interest here was the occasional presence of *Juncus subnodulosus*—usually attributed to secondary mowing-marsh communities—in areas of undoubted primary fen.

The two groups of members interchanged during the course of the morning, and the whole party reassembled at Barton Staithe for lunch.

Afternoon: General tour of some of the Bure valley public broads by hired launch

This tour was mainly intended to provide a final afternoon of somewhat lighter relief after a heavy week's programme of excursions. Starting just above Wroxham Bridge, the launch proceeded downstream and entered successively Wroxham, Salhouse and Hoveton Little Broads. The eroded margins of Wroxham and Salhouse Broads, which lie in the heart of the holiday area, formed a sharp contrast to those of the private or little frequented broads visited earlier in the week; the distinction was less marked in Hoveton Little Broad, which has only very recently been opened to the public.

Still further downstream, the interesting area of Hedney's Bottom (*J. Ecol.* **39**, 1951, pp. 139–41) was passed. This is the site of a small extinct broad lying near the river in the Ranworth Marshes, and now covered entirely by fen and carr. The carr is mainly of the swamp or semi-swamp type, with characteristic dead and moribund alders, and the upstretched leafless branches of these could be seen from the launch across the intervening fenland. The launch eventually turned at St Benet's Abbey, and made a direct return upstream, with a break at Horning for tea, to conclude the final expedition of the week.

The Summer Meeting officially ended after breakfast on the following morning (13 July). The Society was fortunate in having excellent weather for the whole of its week in Norfolk, which added much to the enjoyment of the meeting.

J. M. LAMBERT

Acting Local Secretary

AUTUMN MEETING

28–29 September 1951

The meeting was held at the Department of Botany, The University, Manchester, by kind permission of Prof. Harland.

This year we departed from our normal practice of holding the autumn meeting in London by moving north to Manchester. Between 40 and 50 members attended, and accommodation was kindly provided by Dr E. M. Lind, Warden of Ashbourne Hall.

The meeting commenced on the evening of 28 September, a soirée being held at 7 p.m. in the Department of Botany.

An enjoyable evening was spent, a number of interesting exhibits being shown. These were:

E. M. Lind. The Ecology of Oakmere, Cheshire.
M. E. Phillips. Morphology and Ecology of *Eriophorum angustifolium*.
D. J. Carr and P. S. Dixon. The Distribution Maps of Bryophytes occurring in the Shetlands.
E. W. Jones. The Effect of Smoke on Lichens.
G. Scurfield. Woodlands of the South Pennines.
C. K. Berrie. Colour Photographs of Ecological Interest.

The paper-reading meeting was held on 29 September, and was devoted to a Symposium on Bryophyte Ecology. Members of the British Bryological Society were present.

The morning session, with Dr W. B. Turrill in the chair, was opened at 10 a.m. by Mr P. Greig-Smith on 'Some Problems in the Ecology of the Lejeuneaceae'. These are predominantly a tropical group, but occur in temperate regions where the climate is oceanic. In Britain most of the seventeen species belong to the disjunct Macaronesian-Tropical Element. It is likely that during the post-glacial climatic optimum this group was more widespread in Western Europe, due to the requirement of most of its members of high humidity and temperature. The present-day distribution in Britain emphasizes this. The highest concentration of species being where we have the highest values of Ammano's Index of Hygrothermy (south-west Ireland, West Highlands of Scotland, Lake District, North Wales and Cornwall). Some

species depart from this pattern, some extending farther north, others distinctly southern, while some may extend to south-eastern districts.

The paper stimulated an interesting discussion in which Prof. Richards, Dr E. W. Jones and Dr Wallace took part.

The geographical affinities of the bryophytes of Ronas Hill, Shetland was discussed by D. J. Carr and P. S. Dixon. The boreal element is most prominent, succeeded by the following in decreasing order of prominence: temperate, disjunct tropical, cosmopolitan, arctic alpine, subatlantic, bipolar, disjunct boreal and macaronesian. No endemic species are present emphasizing the youthfulness of the flora.

This paper was followed by a paper by Prof. P. W. Richards on the 'Rhizoidal attachment as a factor controlling habitat preferences in Mosses'. Among lower plants the mechanical factor of attachment to a substratum may be partly responsible for the presence or absence of certain species in a given habitat and thus in determining the composition of plant communities. The importance of this factor in the ecology of littoral algae exposed to wave action is recognized, but it is often not realized that it plays a part also in the ecology of bryophytes, especially those growing on rock surfaces and trees.

It is not generally understood that bryophytes vary very greatly in rhizoid development, some species having none or very few when 'adult', while others have abundant rhizoids. In the Killarney oakwoods, where steep surfaces are occupied by small species well provided with rhizoids (*Diplophyllum albicans*, etc., on boulders, *Ulota* spp. etc. on trees). On horizontal surfaces these small species tend to be ousted by larger bryophytes with less efficient rhizoidal attachments, e.g. *Dicranum* spp., *Hylocomium brevirostre*, *Rhytidiadelphus loreus*, etc. The relationship of rhizoidal characteristics to habitat is well illustrated by a series of species of *Rhacomitrium*. At one extreme is *R. lanuginosum*, which has very few rhizoids except when young and is mainly found on horizontal surfaces or on slopes where grasses, etc., provide firm anchorage. At the other end of the series is *R. aciculare* which has many rhizoids and grows on boulders in swift streams, where it can withstand strong currents. Some byrophytes which are characteristic of stream-beds and the neighbourhood of waterfalls but never grow where water actually flows over them may be limited in their distribution on the one hand by the need for a very wet environment and on the other hand by the inefficiency of their rhizoidal attachments. The important and wide implications of the kind and effectiveness of the rhizoidal attachment in mosses was fully discussed by Dr E. W. Jones, Dr Bell and Mr A. D. Banwell.

The morning meeting was terminated with a paper by Dr E. W. Jones. Dr Jones pointed out that communities of bryophytes and lichens, particularly growing on trunks of trees, are more affected by the aerial environment than are communities of phanerogams. Lichens, in particular, are very sensitive to smoke. Thus the trunks of trees in industrial cities are often bare of lichens but as with increasing distance from sources, e.g. atmospheric pollution, crustose lichens make their first appearance, usually at the base of trunks, followed by foliose, then finally fructicose and corticose lichens. Favoured sites on trees are upper surfaces of leaning trunks or the enlarging bases of trunks, probably due to their favourable water supplies and humidity.

Dr Jones made interesting comparisons between his work and that of C. H. Thorold in Nigeria on epiphytic communities of the trunks of cocoa, considered in relation to rainfall. He has shown how with decreasing dryness (from known rainfall data) there is a succession of the following communities; lichens—hepatics—mosses and phanerogams. The surprising finding that the hepatics were more drought-resistant than the mosses, is probably due to the presence of one or at the most two drought-tolerant species, *Cheilolejeunia* sp. and *Mastigolejeunia carinata*.

A lively discussion followed in which the following members took part: Dr Schelpe, Prof. Valentine, Dr Wanstall, Prof. Richards, Mr J. D. Carr, Dr Lind, Mr Parker and Dr R. E. Hughes.

The afternoon meeting commenced at 2 p.m. with a paper by Prof. A. R. Gemmell on 'Some aspects of the Hawaiian moss flora'. Prof. Gemmell analysed Bartram's *Manual of Hawaiian Mosses*, and it was shown that of the 174 species listed 106 (61 %) were endemic to the archipelago and 68 (39 %) were of wide distribution outside the archipelago. If the sexual mechanism of wide species be examined it is found that 27 species are monoecious, 19 dioecious and 22 are sterile (i.e. no sporogonia have been found). The endemic species, on the other hand, consist of 41 dioecious, 37 sterile, and 28 monoecious species. This increase in the number of dioecious endemic species seems to indicate that evolution of species on the islands has been from dioecious parents rather than monoecious.

Further, it is possible to calculate the number of islands on which an average dioecious or monoecious species occurs and the following table expresses these findings:

Number of island appearances per species

	Endemic	Wide	Endemic minus wide
Monoecious	2·6	2·3	0·3
Dioecious	3·5	2·9	0·6
Sterile	1·8	1·7	0·1

It is argued that since endemic species presumably arose from 'wide' species, the difference between the number of island appearances of 'wide' and endemic is an indication of the degree of adaptive selection in the sexual groups and it can be seen that this is greatest in the dioecious group, and least in the sterile group. Thus an out breeding system has considerable evolutionary advantage.

An examination of the world distribution of the 'wide' Hawaiian species shows that all but two of these species occur in the Malay-Australasian area, thus indicating that the Hawaiian moss flora and that of the above area had a common origin, or that one is derived from the other. In the discussion that followed, Dr W. B. Turrill, Prof. Richards, Dr Baker, Mr Greig-Smith, Dr Bell and Dr E. Schelpe took part.

Dr P. R. Bell then gave a stimulating account of his expedition to South America, in which he described some Andean Bryophyte communities. The paper was well illustrated with coloured photographs.

An account of the ecology of Bryophyte communities of the chalk grasslands of the central north downs was given by Miss M. Cornish. In accordance with expectation the north slopes were most favourable for bryophyte growth. Slope was also stressed as being a major factor, as steep slopes were hotter and heavily grazed. *Festuca ovina* on such sites would be influenced by the development of terraces on Preston Hill and the species of the latter kind of site were compared with those of ungrazed gentle slopes. Similar terraced sites occur on Boxhill, but here certain rarities occur (*Frullania tamarisci*, *Scapania aspera*, *Torella tortuosa*) and these were transplanted on Preston Hill. The latter species survived during the summer at Preston Hill, suggesting that its presence at Boxhill was due to chance distribution.

Miss Cornish also discussed comparatively the bryophyte communities of *Festucetum ovinae*, *Brometum erecti* on old and recent arable, and cleaned scrub on the North Downs. She concluded that:

(1) Percentage byrophyte cover seems to be greatest on disturbed sites with open communities, or on northern slopes (some species are confined to them).

(2) The richness of the flora partly depends on the openness of the habitat, but also on age and part treatment of the community. *Festucetum ovinae* contains the richest bryophyte flora, *Brometum erecti* the least.

(3) Some of the rarer calcicoles (*Ditrichum flexicaule* and *Entodon orthocarpus*) are found only in *Festucetum ovinae* and apparently fail to enter disturbed sites, although conditions seem favourable. Similarly, other species may be found in *Festucetum* and in *Brometum*, but absent in disturbed sites, while others are present in the latter but absent from *Brometum*. The disturbed sites are characterized by a very complete cover of pleurocarpus mosses and the extreme poverty of the flora.

Considerable discussion accrued from this paper in which Dr E. W. Jones, Dr D. J. Carr, Prof. Richards, Dr Bell, Dr Wallace and Dr Turrill took part.

The meeting was terminated by Dr E. Schelpe reading a paper on the ecology of bryophytes in arable land in the Oxford district. Dr Schelpe showed how bryophytes are able to survive on arable land following ploughing, doing so by propagules such as spores and gemmae. Light and depth of burial are important factors in determining survival, rather than carbon dioxide content of the soil air.

The growth of a bryophyte population under a crop is partly governed by the light-intensity. From culture experiments the optimum light intensity appears to be less than one-third full daylight, and that reaching the soil surface falls within this range.

Bryophytes grow rapidly in summer, drought being inimical, and excluding many hepatics, mosses surviving long periods of drought.

During the autumn in unploughed fields, light intensity at the soil surface is markedly reduced by growth of weeds or overwintering crops. The annuals then die out, and the perennials markedly decrease, only shade tolerant species surviving.

The 'calcicole' and 'calcifuge' nature of certain species was studied; both culture experiments and field observations showed the respective preferences of such species to high or low exchangeable calcium and pH in their growing media.

By using radio-active phosphorus it was shown that the rhizoids of a moss are of little importance in supplying salts to the leafy stems.

In the field study of Bryophyte populations on arable land it was shown that by using a square centimetre quadrat, moss gametophyte populations are aggregated, while colonies of *Riccia* are randomly distributed.

The meeting served to emphasize the considerable range of ecological problems amongst the bryophytes, and the active research that is now in progress on eco-geographical and autecological lines.

The President warmly thanked Prof. Harland and Dr E. M. Lind for the hospitality and Mr Greig-Smith for the excellent local arrangements.

R. E. Hughes

THE ANNUAL GENERAL MEETING

Saturday, 5 January 1952

The Annual General Meeting of the Society was held in the Department of Botany of the University of Oxford, on 5 January 1952. The President, Dr W. B. Turrill, was in the chair, and about 120 members were present.

The minutes of the last Annual General Meeting were read and signed. Apologies for absence were received from Dr H. Godwin, Mr V. S. Summerhayes and Dr Horne.

The report of the Honorary Secretaries on the activities of the past year was read and accepted.

Report of the Honorary Secretaries for the year 1951

The thirty-seventh Annual Meeting of the Society was held on 7 January 1951 at the Department of Botany, University College, London. This was attended by over 90 members. At a soirée on the previous evening various ecological exhibits were shown.

Following the business meeting Dr W. B. Turrill gave his Presidential Address on 'Some Problems of Plant Range and Distribution'. During the afternoon four ecological papers were read.

The Society wishes to thank Prof. W. H. Pearsall for his kindness in permitting it frequently to hold its meeting in his department.

On 3–4 April a meeting was held in the rooms of the Linnean Society, London. The President was in the chair. This two-day meeting at Easter was a departure from normal practice but it was well attended (over 100 being present). Thirteen papers were read, which were of a very varied nature. Miss Ruth Badcock opened the meeting with an account of her work on the ecology of the Hydropsychidae (Trichoptera). She was followed by D. S. Johnson on the location of *Cladocera* within lakes and ponds.

R. S. Fitter gave an interesting account of the environment of towns in relation to the habitat preference of birds. The morning session closed when Captain C. Diver gave a very informative account of the work and aspirations of the Nature Conservancy.

The afternoon session was concerned with papers of an entomological nature, papers being read by M. E. Solomon on the population dynamics of storage pests and C. B. Williams on the relation of changes in insect population to previous weather conditions.

D. W. Morley was unable to give his paper on ants' nests.

On the following day the morning session was opened by G. W. Dimbleby on the history of a north-east Yorkshire moor, dealing in particular with the application of the technique of pollen analysis to mineral soil. This was followed by a paper on the ecology of the Lizard by D. E. Coombe. He discussed the factors determining the distribution of the rarer species there.

The value of statistical methods in the study of secondary forest development in Trinidad was well shown in a paper by P. Greig-Smith. E. W. Jones, also studying tropical forest in Nigeria, stressed the importance of archaeological investigations in determining the developmental status of tropical forests.

The afternoon session was confined to papers of an applied nature. J. D. Ovington discussed some ecological problems of afforestation, particular reference being made to the effect of various tree species

on the course of soil development. William Davies outlined the grassland survey work of the Organization for European Economic Co-operation, with particular reference to a survey of the Mediterranean region.

The meeting terminated with an account by A. Brownlee on the response of cattle to their surroundings during grazing.

The meeting as a whole served to stress the wide range of ecological investigation now being pursued in Britain.

A soirée was held on the evening of 3 April at the Herbarium of the Royal Botanic Gardens, Kew. An excellent range of exhibits had been set out, which were much appreciated by members present. The Society wishes to thank the Director, Sir Edward Salisbury, Dr Turrill, Mr Summerhayes and Mr Hubbard for their hospitality and the very enjoyable evening spent at the Herbarium.

Summer Meeting

The summer meeting was held in Norfolk from 6 to 13 July, and was attended by 66 members. Accommodation was provided at Wymondham College. On the evening of the 6 July the Society was entertained by the Norfolk and Norwich Naturalists' Society at a soirée held in the Norwich Castle Museum.

Three days were spent examining various types of primary succession found in the Norfolk Broads. The following areas were visited. Yare valley, Surlingham fens, Bargate Nature Reserve, Wheatfen of Rockland Broad and the Bure and Ant valleys.

Visits to Scolt Head Island and Blakeney Point with their complex of shingle spit, sand dune and salt marsh, occupied two further days.

The meeting terminated with a tour through Breckland.

The Society was fortunate in having excellent weather for the whole of its week in Norfolk, which added much to the enjoyment of the meeting.

The Society is most grateful to Dr J. M. Lambert for leading the various expeditions and making all the arrangements for travel and accommodation. We are also indebted to members of the Norfolk and Norwich Naturalists' Society for their help in making the meeting both successful and enjoyable.

Autumn Meeting

It has been usual to hold the autumn meeting in London. This year we experimented by holding a meeting in the Department of Botany, Manchester, on 28–29 September. The meeting was a symposium on Bryophyte Ecology, held jointly with the British Bryological Society.

A soirée was held on the evening of 28 September, at which members of the staff at Manchester exhibited material of ecological interest. Those giving papers also exhibited material illustrating their work. Dr W. B. Turrill was chairman for 29 September.

The papers read ranged from those of an eco-geographical nature, read by P. Greig-Smith (Ecology of Lejeuneaceae), D. J. Carr and P.S. Dixon (Bryophtes of Ronas Hill, Shetland) and A. R. Gemmell on the Hawaiian Moss flora, to a more experimental study of the bryophytes of arable land in the Oxford district by E. Schelpe.

Interesting ecological papers were also read by P. W. Richards, E. W. Jones and M. Cornish.

P. R. Bell gave an interesting and well-illustrated account of Andean Bryophytes, following his recent visit to South America.

The Society is indebted to Prof. Harland for his hospitality; to Dr E. M. Lind for arranging accommodation at Ashburne Hall; and P. Greig-Smith for acting as local secretary.

During the year the first part appeared of Vol. 39 of the *Journal of Ecology*. The second part will be published soon. Part one of the current volume is unfortunately out-of-print, but it is hoped that more copies will be reprinted in the not distant future. It contains 203 pages, ten original papers, seven reviews and one contribution to the biological flora. The latter is by N. Woodhead on *Lloydia serotina*.

Both parts have been published of Vol. 20 of the *Journal of Animal Ecology*. The volume consists of 266 pages, twenty-three original papers, nine book reviews, and two sets of notices of publications on animal ecology in the British Isles.

During the year the membership of the Society has increased from 680 to 727, i.e. by 47. Actual new members total 70, while 23 have either ceased membership following resignation, death (4) or have ceased paying their subscription.

The Society records with regret the death of a distinguished member in Prof. F. W. Oliver. It is of interest to note that Prof. Oliver was a foundation member of the Society.

The Society had pleasure in electing Dr O. E. Jennings, of the Carnegie Museum, Pittsburg, to an Honorary Membership in view of his distinguished work and long association with the Society.

An analysis of the present position is as follows:

Total	Receive E.	Receive A.	Receive E. and A.	Associates	Hon. Members
727	508	330	119	5	2

In the absence of Mr Summerhayes, Mr C. E. Hubbard reported on the financial position of the Society. In view of the date of the Annual General Meeting it was not possible to give exact estimates but it was was expected that there would be a deficit on the year's working of about £85. There had been less sales of current and back numbers than in previous years, and the cost of printing had sharply increased. This had caused the Council to increase the price of both the *Journal of Ecology* and that of the *Journal of Animal Ecology* to non-member subscribers by 15*s.* and 10*s.* per volume respectively. The Honorary Treasurer warned the Society that increases in members' subscriptions may be necessary.

In a discussion that followed, certain aspects of the Society's financial position were criticized by Prof. Osborne, Dr Cary-Gilson, Dr Watt, Dr Turrill, Prof. Valentine and Mr J. Chear. Arising out of this discussion it was proposed by Captain C. Diver and seconded by Prof. Osborne that there should be an increase in the prices of back numbers of both *Journals*, and that this should bear a proportional relation to the increases in the prices of the current volumes to non-members. This was carried unanimously. Prof. Osborne, seconded by Dr Watt, also proposed that these increased prices of back numbers should also be chargeable to members of the Society.

The President then proposed the renewal of the following grants: (i) £10 to the Fresh Water Biological Association for 1952, (ii) £5. 5*s.* 0*d.* to the Biological Council, and (iii) £2. 2*s.* 0*d.* to the British Co-ordinating Committee of Societies for Nature Conservation; and that the auditors, Messrs William Norman and Sons, be re-elected. Both these proposals were carried.

Dr Gilson then proposed that £20 be paid to Dr Hobby, for assistance in editing the *Journal of Animal Ecology*. This was approved.

The President then proceeded to the election of officers and members of the council as follows:

President: C. B. Williams.
Vice-Presidents: C. S. Elton (1 year), W. B. Turrill.
Hon. Secretaries: G. C. Varley, R. E. Hughes.
Hon. Treasurers: V. S. Summerhayes, C. E. Hubbard.
Hon. Editors: H. Godwin, H. C. Gilson.
Hon. Editors of Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards.
Council: A. R. Clapham, H. G. Baker, D. E. Coombe, C. Diver, C. Gimmingham, J. L. Harley, J. A. Kitching, Miss J. Lambert, E. D. LeCren, A. MacFadyen, E. W. Russell, A. J. Rutter, M. E. Solomon, D. A. Valentine, A. S. Watt, C. B. Williams.

In the absence of the President, Mr C. Elton took the chair. The Society then received the report on the position of the *Journals*. Dr Gilson pointed out that he had only been concerned with the second part of the volume which had appeared in 1951. The first part of Vol. 21 would soon appear and it would contain ten papers.

Prof. A. R. Clapham them commented on the position of the Biological Flora. Only one contribution had appeared during the year (N. Woodhead on *Lloydia serotina*). Other contributions would appear in the second part of Vol. 39. He appealed for further accounts, as progress was very slow.

The Chairman then opened the discussion on the question of the continuation or not of notices of publications on the animal ecology of the British Isles which appear in the *Journal of Animal Ecology*. A lively and long discussion ensued in which opinions were expressed both in favour and against the continuation of these notices. The following members took part: Dr D. Lack, Dr Russell Hall, Dr Yapp, Captain C. Diver, Dr Fitter, Miss Lowe, Major Hume, Prof. Varley, Dr Baker, Mr Elton and Dr Cary-

Gilson. The majority of the speakers stressed the value of these notices, while Dr Cary-Gilson doubted their value, and the sale of separates was small. He mentioned that works of a more physiological nature done abroad would be of greater value, but this would require the setting up of a large organization to deal with them.

The Chairman then proposed that the notices be continued in some form, which could be left to Dr Gilson the Editor. This proposal was carried. After an interval for coffee Prof. G. C. Varley at 11.45 a.m. opened the Symposium on population problems with a paper on 'Population Dynamics in Insects'.

In studying populations Prof. Varley pointed out that his working hypothesis is that the population density of an animal or plant community is governed by its reproductive rate, and by the fraction of the young surviving to reproduce, and that density-dependent factors must operate if the population is to avoid extermination and yet not reach infinite size. The papers of Park on *Tribolium* and Nicholson on *Lucilia* were used to illustrate competitive effects of food limitation. The large-scale changes in the insect populations of the German forests described by Schwerdtfeger were compared with those of mice and lemmings, and the effects of natural control and biological control measures on crop pests were illustrated from the work of Van der Vecht, T. H. C. Taylor and Ullyett. It was concluded that parasites must play a very important role in the control of insect population densities and that an efficient parasite must have the following properties:

(1) It must be able to find many hosts even at low density.

(2) It must have a life cycle synchronized with that of the host so that it searches for hosts when they are available.

(3) It must search where hosts are.

(4) It must itself suffer from no heavy mortality.

The relatively ineffective parasitism of the winter moth was discussed in the light of these criteria.

The effects of weather on insect populations are very great, and Davidson and Andrewartha, and more recently C. B. Williams, have had considerable success in correlating the numbers of trapped insects with present and past weather conditions. This is to be expected since climatic factors influence rates of development, activity, mortality and longevity, and in no way conflicts with a belief in the importance of density dependent factors.

In the energy chain, sunlight—plant—caterpillar—parasite the abundance of any species depends on the abundance of its source of energy, its own efficiency in getting it, and its ability to avoid loss to the next link in the chain. If, for instance, parasites are effective in controlling the caterpillars, the plant will be little damaged. Under these conditions limited food or energy supply is acting as a density dependent factor on alternate members of the chain (on the parasites and on the plants). If an efficient hyperparasite is added to the end of the chain, the results will be quite different. The parasites will be quite ineffective, the caterpillars abundant and the plants heavily damaged. Then density dependent limitation would be effective on the hyperparasites and the caterpillars.

Prof. Varley concluded that this over-simplified scheme illustrates in principle the way in which the idea of density-dependent factors can be used to interpret field results.

Prof. Varley was followed immediately by a paper by Dr A. S. Watt on 'Competition and the Structure of the Community'. The case of two species dominating each other in different parts of the same habitat is presented in *Pteridium* v. *Calluna* on podsolized sand in Breckland. Bracken radiating centrifugally shows a marginal belt of large plants with parallel axes and fronds of the same morphological age forming zones parallel to the advancing front. Such a front advances on *Callunetum* and suppresses the *Calluna*. Behind the marginal belt the bracken opens out becoming patchy, and the individual plants and fronds are smaller. In the open places heather becomes established and spreads, suppressing the bracken, although not to extinction.

Each of the heather- and bracken-dominated communities shows phases which are related to each other in a time sequence. When heather spreads and suppresses bracken, the surviving fronds are found in all phases, but they are not distributed at random: there are more fronds than expected in the weakly defensive initial and degenerate phases, and fewer in the vigorous building and mature. That is, the number of fronds diminishes as the competitive power of the *Calluna* increases especially during the building phase, to increase again on the death of the *Calluna* bush. There is therefore adjustment between these two at the species level.

Nor is this all. The fronds of different morphological age and characteristic of the different phases of the bracken community are distinguishable by their dimensions, in particular by the ratio lamina : petiole. Their distribution in the *Callunetum* shows a high correlation between the phases of the *Callunetum* and the fronds proper to the corresponding phase in bracken. That is, there is a correlation at the 'individual' level. These conclusions are of value in helping us to decide on the nature of the plant community.

The afternoon meeting was opened at 2 p.m. with a brief discussion of the morning papers in which Prof. J. B. Cragg, Dr Watt, Dr Turrill and Prof. Varley took part. Prof. Cragg stressed the lack of accord between experimental results with insect populations and those obtained under field conditions.

The first paper of the afternoon was by Miss E. M. Burrows and Miss S. M. Lodge on 'Intertidal Plant Populations'. Under normal shore conditions, the three species of the genus *Fucus*, *F. spiralis* L., *F. vesiculosus* L. and *F. serratus* L., are readily distinguished, but plants occur which are not easily referable to any of these species. In re-population experiments complete clearance has shown that a zoned covering of these three species is a climax vegetation for a shore in which the substrate is a rock surface or consisting of large boulders where the exposure is not extreme; partial clearance experiments have demonstrated that intense competition among the three species limits their ranges and produces the zonation.

Conditions of algal growth make it difficult to apply to the genus *Fucus* methods used in studying variation among flowering plants. It has been shown however that habitat variation, genetical variation and hybridization occur among the species of the genus. Of particular interest were the results of a zoological experiment carried out at Port St Mary, Isle of Man; the shore at the time of the experiment was mainly bare of algae but covered by *Balanus* and *Patella*. Removal of *Patella* over a broad strip down the shore allowed the development of algal spores and as a stage in the recolonization of the area, a fucoid population appeared in which there was little zonation and in which 60 % of the plants seemed to be hybrid in nature. Wilmott's method (1950) for the study of critical groups has been adapted for analysing and recording the character combinations found among *Fucus* populations. A diagram is constructed for each population using the modal value on a scale of 10 degrees for each of 15 characters studied in 50 perfect plants fruiting for the second time. The characters and the scales are chosen to cover definitions of all the species involved and the full range of variation for each character. If the details of a schedule of the kind suggested here could be agreed upon, it could be used by workers in different parts of the country with the assurance that the results obtained would be strictly comparable. It might then be possible to work out the geographical distribution of character combinations for the whole of the British coast and obtain important information concerning the spread of characters for the genus. In the discussion that followed Dr H. G. Baker questioned the double weighting of inherited sex characteristics. Miss Lodge considered that these were the only ones of value, and were therefore weighted. Prof. Valentine suggested that the introgressive hybridization was in progress within the hybrid *Fucus* populations. The histograms shown by Miss Burrows suggested the transfer of one set of genes from one species to the other: Prof. Varley and Dr Cary-Gilson also took part in the discussion.

Dr D. Lack then followed with a discussion on population dynamics in birds. The few available long-term bird censuses show that nearly all bird populations exhibit restricted and irregular fluctuations, which are extremely small in comparison with the potential rate of increase of the species. Such regulation of populations can be brought about only through the operation of density dependent factors. The effect of the latter on the reproductive rate is very slight, if present at all. All the evidence suggests that the clutch-size of birds corresponds to the average maximum number of young for which they can find enough food. One must therefore look to mortality factors for the main cause of density limitation. The annual adult mortality in birds is high, varying from 30 to 60 % in most species, and it is largely independent of age. There is as yet no direct evidence as to which mortality factors may be the most important, but the indirect evidence is in favour of food shortage for most species and predation for certain gallinaceous birds. Disease seems unlikely to be an important primary cause of death. In addition, birds modify their population density through their behaviour, particularly through migration, irruption and territory. In the discussion that followed the importance of predators was stressed. Dr Middleton, Dr Bell and Dr Fraser-Darling took part.

Dr G. D. H. Bell then gave his paper on 'Population Studies on Certain Arable Crops'. The significance of population studies in arable crops is that the yield of produce can be affected not only by the number

of plants per unit area, but also by their spacing. The special conditions imposed by cultivation tend to diminish some of the effects of the natural environment on plant growth, and this, combined with the genetic constitution of the plant population composing an agricultural variety, has the general effect of increasing the effect of plant population on yield. Population status cannot be divorced from the growing conditions, nor from the nature of the variety, when analysing the contributory causes to variation in yield potential.

In spacing and census work with cereals, it has been shown quite clearly that varietal yields are affected by a number of morphological and developmental characters which in turn are affected by plant density and spacing. The effects of uneven plant spacing in the field (which is the rule with cereals) with variation in plant density, are not the same with different varieties and under dissimilar growing conditions, while it is also true that yield is unaffected by plant population densities over a wide range of total plant numbers. The frequent lack of any direct relationship between total yield and plant number and contradictory results under different conditions of experiment, is due to the differential capacity of individual plants to compensate by increased growth for reduced plant number.

In the case of the spaced root crops such as sugar beet, competition is reduced by singling. There is much evidence to show that the highest yields and the best quality of beets are obtained from higher plant populations although growing conditions have a strong effect on production at different plant densities. Uniformity of plant distribution is also important, but as standards of cultivation and production are varied, population factors become of less significance. In the discussion that followed Dr E. W. Jones compared Dr Bell's observations with similar studies on trees.

A paper was then read by Mrs Stella S. Williams on 'Changes in the Plant Population of Leys during the Establishment Phase'. The early work done at the Welsh Plant Breeding Station showed that there was much variation in sensitivity to external conditions amongst grass and clover species. Their work also dealt with the causes of mortality. Observations were not made at sufficient frequency to trace the history of individual seedlings.

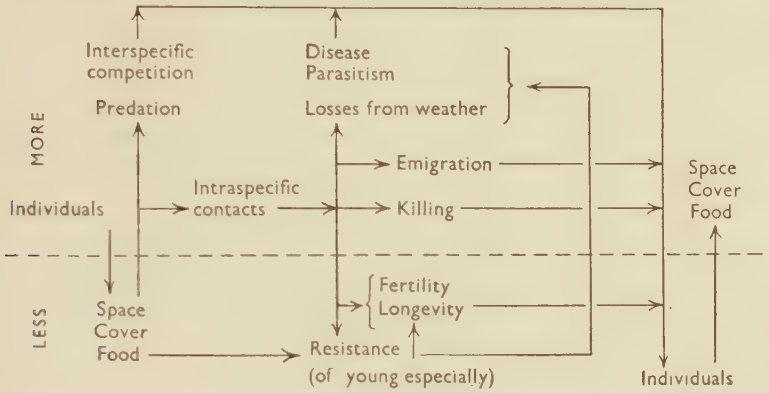
Similar experiments were started at the Grassland Research Station in 1947. Germination and mortality were traced by means of frequently pantographed charts of permanent quadrats on simple mixtures sown in four seasons. The mixtures were S. 23, *Lolium perenne*, with S. 100, *Trifolium repens*, and S. 48, *Phleum pratense*, also with S. 100. The method proved unsatisfactory for the study of *Trifolium*. The results confirmed the tendency to late germination of *Phleum* and its greater sensitivity to external conditions particularly compared with that of *Lolium*. Both species are however, vulnerable to soil cracking arising from the low moisture content of the soil. In both cases the established sward was composed of seedlings of different ages, although the survival from early germination was higher than that from later germination. The causes of mortality include competition, drought and the effects of soil fauna and grazing animals. A high plant density of a cover crop or of *Phleum* seedlings themselves, protects the smaller *Phleum* seedlings from the most severe effects of drought. The 'protecting' cover crop or larger *Phleum* seedlings have longer roots than the more sensitive seedlings and are, therefore, able to draw on a deeper layer of soil for their water requirements.

Dr Watt called attention to the importance of root studies in relation to problems of this kind. Mr Cooper stressed the importance of taking into account the genetic type within the species and agricultural variety, as considerable variation in resistance to the adverse environment could be expected. Dr D. H. Chitty then proceeded to give the final paper in the Symposium on 'Population Dynamics in Mammals'. Dr Chitty pointed out that it is reasonable to suppose that a species which frequently exhausted its food supply might be supplanted by one whose population densities were controlled at a safer level. He therefore discussed alternatives to population control through starvation. As numbers increase, a high proportion of individuals may be destroyed by predators and through competition with other species. More contacts between individuals should favour the spread of parasites and disease, and animals which are driven into unfavourable parts of the habitat may die from exposure. Losses may be expected from fighting and emigration, and fertility and longevity may be reduced directly or through changes in age structure.

In some species, however, periodic reduction in numbers is far greater than can be explained in these ways. An abnormally high mortality rate, particularly among the younger generations, may persist for some time after a period of abundance has passed and the environment is no longer unfavourable.

Dr Chitty's evidence suggested than an abnormal physiological condition is produced by frequent contacts between individuals and that their descendants are not fully viable. Mr J. R. Clarke has shown that physiological changes, typical of Slye's adaptation syndrome, result from fighting among field voles; but it is not yet proved that such females produce abnormal young.

Populations might be controlled by any one process in which the mortality rate increased with abundance; but it is more likely that several processes are usually involved, their relative importance varying according to the species and habitat. Dr Chitty's conclusions are schematized in the following diagram:



A very lively and interesting discussion followed, in which physiological adjustments in both man and animals to adverse environmental conditions (particularly overcrowding) were discussed. Major Hume, Dr Clark, Dr Solomon and Prof. Varley took part in the discussion.

At the conclusion of the meeting Dr W. B. Turrill expressed the hearty thanks of the Society to our hosts Prof. Osborne and his colleagues, and also to Prof. Varley for organizing the Symposium and for arranging accommodation for members at Jesus College.

The Annual General Meeting was preceded on Friday evening by a very enjoyable soirée at the Department of Botany.

Exhibits included:

Prof. J. L. Harley and colleagues. Phosphorus uptake by mycorrhizal roots of the beech.

Dr F. H. Whitehead. Field determination of wind velocity at various levels, and the use of electrical soil moisture meters.

Mr A. D. Bradshaw. Ecotypic differentiation in *Agrostis*.

Mrs S. S. Williams. Population studies on *Lolium* and *Phleum*.

There were also exhibits by Prof. Varley, Dr Elton and Dr Chitty illustrating the population work in progress at Oxford.

R. E. Hughes

LIST OF MEMBERS (30 MAY 1952)

E. = Takes *The Journal of Ecology.* A. = Takes *The Journal of Animal Ecology.*

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, R. E. HUGHES, School of Agriculture, Downing Street, Cambridge

E. **Abdin**, Dr G., M.Sc.; Botany Dept., Faculty of Science, Fouad I University, Abbassieh, Cairo, Egypt.
E. **Abeywickrama**, B.A., B.Sc.; Department of Botany, University of Ceylon, Colombo, Ceylon.
E. A. **Adams**, Dr Charles C.; 149 Manning Boulevard, Albany 3, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
E. A. **Airey** A. F., M.B.O.U.; 87 South Promenade, St Annes on Sea, Lancs.
E. A. **Airy Shaw**, H. K., B.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Allee**, Prof. W. C.; 114 Leigh Hall, University of Florida, Gainsville, Florida, U.S.A.
A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
E. **Allison**, Miss I. J., B.A.; 11 High Street, Sandy, Beds.
E. **Allott**, D. J.; 167 Covington Way, Norbury, London, S.W. 16.
E. **Alston**, A. H. G., M.A.; 25 Pelham Crescent, London, S.W. 7.
E. **Anderson**, J. A. R., B.Sc.; Forestry Dept., Sibu, Sarawak.
E. **Andrews**, F. W., D.Sc., Ph.D.; 27 Minterne Avenue, Norwood Green, Southall, Middlesex.
E. **Archibald**, Miss E. E. A., M.Sc.; 42, 13th Avenue, Walmer, Port Elizabeth, S. Africa.
E. **Armitage**, Miss E.; Foxdale, nr Ross, Herefordshire.
Ash, J. S., B.Sc., M.B.O.U.; I.C.I. Game Research Station, Burgate Manor, Fordingbridge, Hants. (*Associate Member*).
E. **Ashby**, Dr Eric; The Queen's University, Belfast.
Ashby, K. R., B.A.; Zoology Dept., The University, South Road, Durham (*Associate Member*).
E. **Ashby**, Dr M.; 2 Redlands, Tiverton, Devon.
E. **Asprey**, Prof. G. F.; The University College of the West Indies, Kingston, Jamaica.
E. A. **Audy**, J. R., M.B., B.Sc.; Dept. of Entomology, London School of Hygiene and Tropical Medicine, Keppel Street, London, W.C. 1.
A. **Auerbach**, Dr S. I.; 4450 N. Sawyer Avenue, Chicago 25, Illinois, U.S.A.
E. **Austwick**, P. K. C., B.Sc.; Mount MacGregor, 29 Surrender Crescent, Brighton 6.
E. **Backhouse**, G. W., B.Sc.; Forestry Commission, Brooklands Avenue, Cambridge.
E. **Bacon**, Mrs Alice, B.Sc.; Biological Dept., The Technical College, Brighton.
A. **Badcock**, Miss R. M., M.Sc.; Department of Zoology, The University, Glasgow, W. 2.
E. A. **Bagenal**, T.; Marine Station, Keppel Pier, Millport, Isle of Cumbrae, Scotland.
E. A. **Baker**, H. G., Ph.D.; Botany Dept., The University, Leeds 2.
E. **Balfour**, Mrs E. J.; Newton Hall, Windygates, Fife.
A. **Balfour-Browne**, W. A. F., M.A., F.R.S.E.; Brocklehirst, Collin, Dumfries, Scotland.
E. **Ballantine**, Miss D., B.Sc.; 'Priors Close', Cambo Place, Cullercoats, Northumberland.
E. **Ballard**, F., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Bally**, P. R. O.; Botanist, Coryndon Memorial Museum, Nairobi, Kenya, E. Africa.
E. **Balme**, Miss O. E., B.Sc.; Imp. Coll. Field Station, Silwood Park, Sunningdale.
A. **Band**, R. M.; 516 North Drive, Cleveleys, nr Blackpool, Lancs.
A. **Barker**, T. W., B.Sc.; 346 Stones Villas, Walsden, Todmorden, Lancs.
E. **Barkley**, Miss S. Y., B.Sc.; 42 Ovington Square, London, S.W. 3.
E. **Barnes**, B., D.Sc., Ph.D.; Dept. of Biology, Chelsea Polytechnic, Manresa Road, London, S.W. 3.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Barnes**, Mrs M., M.Sc.; Lorne Villa, The Marine Parade, Millport, Isle of Cumbrae, Scotland.
E. A. **Barrett**, J. H., B.A.; Dale Fort Field Centre, Haverfordwest, Pembrokeshire.
E. **Barry**, D. H., B.Sc.; 7 Tring Avenue, Ealing Common, W. 5.

E. **Barton**, Miss Frances M.; 19 Park Street, Bath.

Bateman, Miss L. M. E.; 'Chislehurst', 3 West Park Street, Dewsbury, Yorks. (*Associate Member*).

E. A. **Bates**, Dr Marston; The Rockefeller Foundation, 49 West 49 Street, New York City 20, U.S.A.

E. **Baxter**, Miss E. V., F.L.S.; The Grove, Upper Largo, Fife.

E. **Bayer**, Prof. A. W., D.Sc.; Dept. of Botany, Natal University College, Pietermaritzburg, S. Africa.

E. **Beard**, Dr J.; Natal Tanning Extract Co. Ltd., Pietermaritzburg, Natal, S. Africa.

E. **Beddows**, A. R., M.Sc.; Welsh Plant Breeding Station, Penglais, Aberystwyth.

E. **Bell**, Dr G. D. H.; University School of Agriculture, Cambridge.

E. **Bell**, Prof. H. P.; Botanical Laboratory, Dalhousie University, Halifax, Nova Scotia.

E. A. **Bentley**, Dr E. W., F.R.E.S.; 41 Cumberland Road, Bromley, Kent.

A. **Berg**, Dr Kaj; Freshwater Biological Laboratory, Hillerød, Denmark.

A. **Bertram**, Dr G. C. L.; St John's College, Cambridge.

E. A. **Bexon**, Miss D., M.Sc.; University College, Nottingham.

E. **Bhâradwâja**, Prof. Y., M.Sc., Ph.D.; Dept. of Botany, Benares Hindu University, Benares 5, India.

E. **Bharucha**, Dr F. R.; 6 Alexandria Road, New Gamdevi, Bombay 7, India.

E. **Bingley**, F. J., M.A.; Flatford Mill Field Centre, East Bergholt, nr Colchester, Essex.

A. **Birch**, L. C., M.Sc.; Zoology Dept., University of Sydney, N.S.W., Australia.

E. **Birmingham Natural History and Philosophical Society**; 114 Oxford Road, Moseley, Birmingham 13 (C. E. A. Andrews, B.Sc., F.L.S., *Hon. Treasurer*).

E. **Birse**, E. L., B.Sc.; Imp. College of Tropical Agriculture, St Augustine, Trinidad, B.W.I.

E. A. **Blackburn**, Miss K. B., D.Sc.; Botanical Dept., King's College, Newcastle-upon-Tyne 2.

E. **Blackman**, Prof. G. E.; Univ. Dept. of Agriculture, Oxford.

E. **Blanchard**, Miss B., B.Sc.; Hartley Botanical Laboratories, The University, Liverpool 3.

E. **Blank**, T. H., B.Sc.; 'The Limes', Damerham, nr Fordingbridge, Hants.

A. **Bletchly**, J. D., B.A.; c/o Lloyds Bank, Nailsworth, Glos.

E. **Bloomer**, H. H.; 'Longdown', Sunnydale Road, Swanage, Dorset.

E. **Boatman**, D. J., B.Sc.; 7 Hurst Road, Buckhurst Hill, Essex.

E. **Böcher**, Dr Tyge W.; Universitetets Planteanatomiske Laboratorium, Gothersgade 140, Copenhagen K, Denmark.

E. **Bogdan**, A. V.; P.O. Box 338, Dept. of Agriculture, Nairobi, Kenya Colony.

A. **Booth**, Capt. B. D. McDonald; Royal Scots Greys, B.A.O.R. 8.

E. **Bor**, N. L., C.I.E., M.A., D.Sc., F.L.S.; Royal Botanic Gardens, Kew, Surrey.

E. **Boughey**, Prof. A. S.; University College, Achimota, Accra, Gold Coast.

A. **Bovey**, Prof. P.; Entomologisches Institut der Eidg. Tech. Hochschule, Universitätstrasse 2, Zürich, Switzerland.

E. A. **Bowyer**, F. H., M.B.E.; Barclay Perkins & Co. Ltd., Park Street, Southwark, London, S.E. 1.

A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.

E. **Boyko**, Dr H.; Ministry of Agriculture, Ha' kirya, Tel-Aviv, Israel.

E. **Bradshaw**, A. D., B.A.; Dept. of Agricultural Botany, Bangor, N. Wales.

E. **Braid**, Major K. W., M.A., B.Sc.; West of Scotland Agricultural College, 6 Blythswood Square, Glasgow.

E. **Braun**, Miss E. L.; Salem Pike, Mt. Washington, R.R. 13, Box 41 C, Cincinnati 30, Ohio, U.S.A.

E. **Braun-Blanquet**, Dr J.; Station de Recherches géobotaniques, Chemin du Pioch de Boutonnet, Montpellier, France.

E. **Brenchley**, Dr Winifred E., O.B.E.; Rothamsted Experimental Station, Harpenden, Herts.

E. **Brett**, D. W.; 43 Penrhyn Avenue, Walthamstow, London, E. 17.

E. **Brett**, Miss O. E., B.Sc.; 13 The Vale, Woodford Green, Essex.

E. **Brewer**, Prof. H. E.; Department of Botany, State College of Washington, Pullman, Washington, U.S.A.

E. A. **Brian**, M. V., M.A.; Zoology Dept., The University, Glasgow, W. 2.

E. **Brien**, T. R., B.Sc.; 7 Orange Hill Road, Prestwich, Manchester.

E. **Brierley**, J. K., B.Sc.; 'Greenways', Lilac Avenue, Kingsway, Derby.

E. **Bristol Naturalists' Society**, Botanical Section; c/o Bristol Nat. Library, City Museum, Queens Road, Bristol.

A. **Brown**, A. G., M.R.C.S., L.R.C.P.; Colac, Victoria, Australia.
A. **Brown**, E. B., B.A.; 'Oakleigh', Chittering, Waterbeach, Cambs.
A. **Brown**, E. S., B.A.; Hailey Lodge, Hertford Heath, Hertford.
A. **Brown**, Miss F. M.; West Riding Rivers Board, 71 Northgate, Wakefield, Yorks.
E. **Brown**, J. M. B., B.Sc.; Imperial Forestry Institute, South Parks Road, Oxford.
A. **Brown**, P. E.; Woodside, Baughurst, Basingstoke, Hants.
A. **Brown**, V. M., B.Sc.; 43 Kensington Gdns, Darlington.
A. **Brownlee**, A., B.Sc.; A.R.C. Field Station, Compton, nr Newbury, Berks.
E. A. **Bullock**, A. A., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. A. **Bullock**, W. A. C., B.Sc.; 2, The Pastures, Repton, Derby.
E. **Bulman**, Mrs M.; Wentworth House, Chesterton Lane, Cambridge.
E. A. **Burckhardt**, D.; Sevogelstrasse 81, Basel, Switzerland.
E. **Burges**, Prof. N. A., M.Sc., Ph.D.; Botany Dept., University of Sydney, N.S.W., Australia.
E. **Burkill**, I. H., M.A.; Clova, The Mount, Leatherhead, Surrey.
E. **Burman**, A. D.; 41 Trinley Road, Knightswood, Glasgow, W. 3.
E. **Burman**, H., A.R.I.C., A.M.I.Chem.E.; 82 Dee Street, Riddrie, Glasgow, E. 1.
E. **Burnett**, Miss E. M., B.Sc.; c/o Mrs N. Matthews, 2 Carden Terrace, Aberdeen, Scotland.
E. **Burrows**, Dr Elsie M.; Hartley Botanical Laboratories, The University, Liverpool 3.
E. **Burton**, Dr Marie, 515 Tonbridge Road, Maidstone, Kent.
E. A. **Burtt**, B. L., B.Sc.; Royal Bot. Gardens, Edinburgh 4.
A. **Bush**, Dr S. F.; Dept. of Zoology, Natal University College, Pietermaritzburg, S. Africa.
E. **Butcher**, Dr R. W., B.Sc.; Culford House, Ewe Lamb Lane, Bramcote, Notts.
A. **Butler**, Dr C. G.; Rothamsted Experimental Station, Harpenden, Herts.
E. A. **Butler**, F. H. C., M.A., M.Sc.; Ravensmead, Keston, Kent.
A. **Buxton**, A. P.; Virus Research Institute, P.O. Box 49, Entebbe, Uganda.
E. A. **Buxton**, Lt.-Col. E. N., B.A., M.C.; Wallsgrove House, High Beach, Loughton, Essex.
A. **Buxton**, Prof. P. A., F.R.S.; London School of Hygiene, Keppel Street, London, W.C. 1.
E. **Caldwell**, Prof. J., D.Sc., Ph.D.; Dept. of Botany, University College of the South-West, Exeter.
E. **Callens**, Rev. Fr. Hubert; Jardin Gillet, Kisantu, Belgian Congo.
A. **Campbell**, B., B.Sc.; British Trust for Ornithology, 91 Banbury Road, Oxford.
E. **Campbell**, Miss M. S., F.L.S.; 29 Burnsall Street, London, S.W. 3.
E. A. **Carpenter**, K.; 'Broad Gates', Bird Green, Beachamp Roding, Essex.
A. **Carpenter**, Prof. K. E., Ph.D.; Zoology Dept., University of Liverpool.
E. **Carson**, Dr G. P.; 2 Chesterton Hall Crescent, Cambridge.
A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
E. A. **Carter**, J. E., M.A.; 38 Kennington Road, Fulwood, Preston, Lancs.
E. **Carter**, Dr Nellie; 23 Mount Side, Guildford, Surrey.
E. A. **Castell**, C. P., B.Sc.; 52 Graham Road, Wimbledon, London, S.W. 19.
E. **Chalklin**, Miss K. M., M.Sc.; Dept. of Botany, University Science Laboratories, South Road, Durham.
E. A. **Chambers**, Dr V. H., A.R.C.S.; 47 Westbourne Road, Luton, Beds.
E. A. **Champion**, Prof. H. G.; Imperial Forestry Institute, South Parks Road, Oxford.
A. **Chandler**, E. A., B.Sc.; Little Gate Rounds, Newdigate, Surrey.
E. A. **Chapman**, Mrs E. M. H.; c/o Forest Dept., Nicosia, Cyprus.
E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
E. **Chapman**, Prof. V. J., B.A., Ph.D.; Dept. of Botany, Univ. College, Auckland, New Zealand.
E. **Chapple**, J. F. G., F.L.S.; The Brackens, Nicholas Way, Northwood, Middlesex.
E. **Chatto**, A. E.; Weston, White Barn Farm, Elmstead, Colchester, Essex.
E. A. **Chear**, John, F.L.S.; 17 Elmwood, Welwyn Garden City, Herts.
A. **Chitty**, D. H.; Bureau of Animal Population, Botanic Gardens, High Street, Oxford.
E. **Christie**, M. G., B.A.; E.A. Malaria Unit, P.O. Amani, Tanga, Tanganyika, E. Africa.
E. **Clapham**, Prof. A. R.; Botanical Dept., The University, Sheffield 10.
E. **Clark**, W. A., Ph.D.; Dept. of Botany, King's College, Newcastle-upon-Tyne 2.
E. **Clowes**, Dr F. A. L.; Dept. of Botany, South Parks Road, Oxford.
A. **Colquhoun**, M. K.; Common Farm, Blackthorn, Bicester.

E. **Colvin**, Miss B.; 28 Baker Street, London, W. 1.
E. A. **Conder**, P. J.; Dale Fort Field Centre, Haverfordwest, Pembrokeshire.
E. **Conolly**, Miss A. P., M.A.; Botany Dept., University College, Leicester.
E. **Conway**, Mrs E.; Botany Dept., The University, Glasgow, W. 2.
E. **Conway**, Miss V. M., Ph.D.; The Nature Conservancy, 83–91 Victoria Street, London, S.W. 1.
E. **Coombe**, D. E.; Botany School, Downing Street, Cambridge.
E. **Cooper**, J. P., B.Sc.; Dept. of Agricultural Botany, The University, Reading.
E. **Cooper**, Prof. W. S.; 1421 Bluebell Avenue, Boulder, Colorado, U.S.A.
A. **Corbet**, P.S., B.Sc., F.R.E.S.; Dept. of Zoology, Downing Street, Cambridge.
E. **Cornish**, Miss M. W., B.Sc.; 63 Craigen Avenue, Croydon, Surrey.
E. A. **Coulson**, B. W. H.; The School, Oundle, nr Peterborough.
E. **Coulthard**, C. E., M.P.S.; 51 Henry Road, West Bridgford, Nottingham.
A. **Cragg**, Prof. J. B., M.Sc.; Dept. of Zoology, Science Laboratories, South Road, Durham.
E. **Craig**, Miss A. M.; Fronheulog, New Road, Llanelly, Carmarthenshire.
A. **Cramp**, S., B.A.; 9 Queen Court, London, W.C. 1.
E. **Creber**, G. T.; 91 Headstone Lane, North Harrow, Middlesex.
E. **Crespin**, J. F., B.A.; The School, Dartington Hall, S. Devon.
E. **Crocker**, R. L., D.Sc.; Division of Soils, Hilgard Hall, University of California, Berkeley 4, California, U.S.A.
E. **Crowder**, Mrs A. A., B.A.; 25 Donview Road, Aberdeen.
E. **Croydon Natural History and Scientific Society**; 34 Raleigh Avenue, Wallington, Surrey.
E. **Crundwell**, A. C.; Dept. of Botany, The University, Glasgow, W. 2.
E. **Curtis**, Prof. J. T.; Botany Dept., Biology Building, University of Wisconsin, Madison 6, Wis., U.S.A.
E. **Curtis**, Miss W. M., B.Sc.; University of Tasmania, Box 647c, P.G.O. Hobart.
E. **Daggash**, M.; c/o Forest Dept., Kaduna, N. Nigeria.
E. **Dalby**, D. H., B.Sc.; 108 Gordon Road, Camberley, Surrey.
E. A. **Dales**, R. P., Ph.D.; 67 Westmoreland Avenue, Squirrels Heath, Essex.
A. **Dalgety**, C. T.; Lockerley Hall, Romsey, Hants.
E. A. **Dansereau**, Dr P.; Dept. of Botany, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. A. **Darling**, F. F., D.Sc., Ph.D., F.R.S.E.; The Old Rectory, Lilley, Brightwalton, nr Newbury, Berks.
E. **Davey**, Miss A. J., M.Sc.; Dept. of Botany, University College of N. Wales, Bangor, N. Wales.
E. **Davies**, Miss E. W., B.Sc.; Botany Dept., The University, Leeds.
E. A. **Davies**, J. Ll., M.A.; County Planning Dept., Clifton Road, Winchester.
A. **Davies**, O. J. H.; The Oak House, Crossways, Shenfield, Essex.
E. **Davies**, Dr Wm.; Grassland Research Station, Drayton, Stratford-on-Avon, Warwicks.
E. **Davies**, W. C.; The Cawthron Institute, Nelson, New Zealand.
E. **Davis**, A. G., B.S.A., M.Sc.; Wye College, Ashford, Kent.
E. A. **Davis**, D. H. S.; Plague Research Laboratory, P.O. Box 1038, Johannesburg, S. Africa.
E. **Davis**, P. H., B.Sc., F.L.S.; Dept. of Botany, Royal Botanic Gardens, Edinburgh.
E. A. **Davis**, T. A. W.; South Mullock, Haverfordwest, Pembrokeshire.
A. **Davis**, W. B., Ph.D.; Box 254FE, College Station, Texas, U.S.A.
A. **Dawes**, Miss T. M. E., B.Sc.; Dept. of Zoology, University College, Nottingham.
E. **Dawkins**, H. C., M.A.; c/o Forest Dept., Entebbe, Uganda.
A. **Day**, Dr J. H.; Dept. of Zoology, University of Capetown, S. Africa.
A. **Delany**, M. J., B.Sc.; Dept. of Zoology, University College, Exeter.
E. **Dennis**, R. W. G., Ph.D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey,
E. **De Rousset-Hall**, O., M.A.; 44 Great Bowden Road, Market Harborough, Leics.
A. **De Rousset-Hall**, Mrs P. J.; 44 Great Bowden Road, Market Harborough, Leics.
E. A. **Dice**, Lee R., Ph.D.; Institute of Human Biology, 1135E, Catherine Street, Ann Arbor, Michigan, U.S.A.
E. **Dilnot**, Miss J., B.Sc.; 480 Liverpool Road, Birkdale, Southport, Lancs.
E. **Dimbleby**, G. W., M.A., D.Phil.; Imperial Forestry Institute, South Parks Road, Oxford.
E. A. **Diver**, Capt. C., C.B.E.; Nature Conservancy, 83–91 Victoria Street, London, S,W. 1.

A. **Donaldson**, R. P.; Royal Society for Protection of Birds, 82 Victoria Street, London, S.W. 1.
E. **Dony**, J. G., Ph.D.; 41 Somerset Avenue, Luton, Beds.
A. **Dowdeswell**, W. H., M.A.; 5 Kingsgate Street, Winchester.
A. **Driver**, P. M.; Warnless Cottage, Bond End, Upton St Leonards, Gloucester.
E. A. **Drummond**, R. B., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Duffey**, E. A. G., B.Sc.; 4 Church Street, Summertown, Oxford.
A. **Duncan**, Miss A., B.Sc.; Marine Biological Station, Port Erin, Isle of Man.
A. **Duncan**, A. B., B.A.; Lann Hall, Tynron, Dumfries.
E. **Dundas**, J.; Forest Headquarters, Ibadan, Nigeria.
A. **Dunnett**, G. M., B.Sc.; 30 Bonnymuir Place, Aberdeen, Scotland.
E. **Du Rietz**, Prof. Einar; Växtbiologiska Institutionen, Uppsala, Sweden.
E. A. **Dussart**, B. H., D.E.S.; Le Paraclet, par Boves, Somme, France.
E. **Ebuade-Iyamabo**, J. O.; Forest Headquarters, Ibadan, Nigeria.
A. **Edelstam**, Carl G.; Östermalmsgatan 61, Stockholm 5, Sweden.
A. **Edinburgh University Biological Society**, Royal Botanic Gardens, Edinburgh.
E. **Eggeling**, W. J., B.Sc., Ph.D.; Forest Office, Entebbe, Uganda.
E. **Elder**, N. L., M.A., F.R.G.S.; 43 McHardy Street, Havelock North, New Zealand.
E. A. **Elton**, Charles; Dept. of Zoological Field Studies, Botanic Gardens, High Street, Oxford (*Vice-President*).
E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, London, E. 15).
E. **Evans**, Miss E. M., B.Sc.; c/o Mrs Foster, 12 Spring View Road, Sheffield 10.
E. **Evans**, E. Price; The Moorings, Glan-y-Mor Road, Deganwy, Llandudno Jnct., N. Wales.
A. **Evans**, F. C.; Laboratory of Vertebrate Biology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. **Evans**, Dr G. C.; Botany School, Downing Street, Cambridge.
A. **Evans**, Dr Gwilym O.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Falk**, P.; Tudor House, Horton Crescent, Rugby.
E. **Fanshawe**, D. B., B.A.; Forestry Station, Mazaruni, British Guiana.
E. **Fenton**, E. Wyllie, D.Sc.; 13 George Square, Edinburgh.
E. A. **Fenton**, G. R., B.A., B.Sc.; Church Farm, Gringley on the Hill, nr Doncaster.
A. **Fidler**, Dr J. H.; Ministry of Agriculture and Fisheries, University College of S. Wales and Mon., Cathays Park, Cardiff.
E. A. **Fincher**, F.; Randan Wood, Woodcote, Bromsgrove, Worcs.
E. A. **Fisher**, J. M.; Old Rectory, Ashton, Northants.
A. **Fitter**, R. S. R., B.Sc. (Econ.); Greyhounds, Burford, Oxon.
A. **FitzPatrick**, Mrs M. J.; 8 Cumberland Road, Barnes, London, S.W. 13.
E. **Fleming**, Dr G. W. T. H., F.L.S.; Barnwood House, Gloucester.
E. A. **Flemming**, W. J. W., B.A.; Soil Conservation, Public Works, Paeroa, New Zealand.
E. **Foggie**, A., B.Sc.; c/o Chief Conservator of Forests, P.O. Box 527, Accra, Gold Coast.
A. **Ford**, J.; Tsetse Research Dept., Shinyanga, Tanganyika Territory.
E. **Forman**, L. L., B.Sc.; 8 Glendale Avenue, Edgeware, Middlesex.
A. **Forster**, G. R., B.Sc.; Marine Biological Laboratory, Citadel Hill, Plymouth.
E. **Frank**, Dr Erica M.; Box 31, Oak Glen Station, Lansing, Ill., U.S.A.
E. **Fraser**, D. A., B.A.; Forest Insect Laboratory, Sault Ste Marie, Ontario, Canada.
E. **Fraser**, G. K., M.A., D.Sc.; Macaulay Institute, Craigiebuckler, Aberdeen.
A. **Freeman**, Dr J. A.; Ministry of Food Infestation Division, 58 High Holborn, London. W.C. 1.
E. **Frost**, L. C., B.A.; The West Green, Poringland, Norwich, Norfolk.
A. **Frost**, Miss W. E.; The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. **Froud**, M. D., B.Sc.; The College, Wye, Ashford, Kent.
E. **Fulford**, R. M.; Dept. of Botany, The University, Nottingham.
E. **Galt**, R. W. C., B.Sc.; 20 Braid Farm Road, Edinburgh.
E. **Gams**, Dr Helmut; Schneeburggasse 67, Innsbruck-Hötting, Austria.
E. **Gardner**, Dr G.; School of Higher Commercial Studies, 535 Viger Avenue, Montreal, Canada.
E. **Gates**, L. F., B.A.; Dunholme Field Station, Dunholme Holt, Lincoln.

E. **Gayner**, J. S., M.R.C.S.; Hall Cottage, New Earswick, Yorks.
E. A. **Gensch**, R. H., U.S. Fish and Wildlife Service, 1001 Fidelity Buildings, Kansas City 6, Missouri, U.S.A.
E. **George**, Miss B. N., B.A.; Grassland Research Station, Drayton, Stratford-on-Avon.
E. **Germain**, Dr R.; Institut National pour l'Étude Agronomique du Congo Belge, Yangambi, Congo Belge.
E. **Gibby**, Mrs A. N., B.Sc., A.R.I.C.; Prebend's Gate, Quarry Heads Lane, Durham.
E. **Gibson**, Miss C. M.; Trematon, 11 South Leigh Road, Havant, Hants.
A. **Gilbert**, O. J. W., B.Sc.; Zoology Dept., University College, Bangor, N. Wales.
E. **Gilbert-Carter**, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.
E. A. **Gillett**, J. B., M.A.; 40 Pensford Avenue, Richmond, Surrey.
E. **Gillham**, Miss M. E.; 209 Gunnersbury Park, Ealing, London, W. 5.
E. **Gilliland**, Dr H. B.; Dept. of Botany, University of the Witwatersrand, Johannesburg, S. Africa.
E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.
E. **Gilmour**, J. S. L., M.A.; Cory Lodge, Hills Road, Cambridge.
E. **Gilson**, Mrs H. Cary, Ph.D.; The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. **Gilson**, H. Cary; The Ferry House, Far Sawrey, Ambleside, Westmorland, (*Hon. Editor of Journal of Animal Ecology*).
E. **Gimingham**, C. H., B.A., Ph.D.; Dept. of Botany, The University, Old Aberdeen.
E. A. **Glasgow and Andersonian Nat. Hist. and Microscopical Soc.**; Societies' Rooms, Royal Technical College, Glasgow.
A. **Glasgow**, Dr J. P.; Eattrro, P.O. Maseno, via Kisumu, Kenya.
E. A. **Glover**, Major P. E., M.Sc.; c/o EATTRRO, P.O. Box 2141, Nairobi, Kenya.
A. **Godfrey**. Miss G. K.; St Anne's Society, Musgrave House, 1 South Parks Road, Oxford.
E. **Godward**, Dr Maud, B.E.; 8 Deyncourt Gardens, Upminster, Essex.
E. A. **Godwin**, H., Sc.D., F.R.S.; Botany School, Cambridge (*Hon. Editor, Journal of Ecology*).
E. A. **Good**, Prof. R. D'O., M.A., ScD.; Botanical Dept., University College, Hull.
E. **Goodall**, D. W., B.Sc., Ph.D., D.I.C.; Botany School, Melbourne University, Melbourne, N. 3, Australia.
A. **Goodbody**, I. M., B.A.; Natural History Dept., Marischal College, Aberdeen.
A. **Goodhart**, C. B.; 28 St Margaret's Road, Cambridge.
E. **Goodman**, G. T., B.Sc.; 120 Pendre, Bridgend, Glamorgan.
E. **Goodwin**, Du Wayne, L., M.S.; Botany Dept., Washington State College, Pullman, Washington, U.S.A.
E. **Gorham**, Eville, M.Sc.; Dept. of Botany, University College, Gower Street, London, W.C. 1.
A. **Gradwell**, G. R., M.A.; Hope Dept. of Entomology, University Museum, Oxford.
E. **Green**, P. S., B.Sc.; Royal Botanic Garden, Edinburgh 4.
E. **Greenway**, P. J., F.L.S.; East African Herbarium, P.O. Box 5166, Nairobi, Kenya Colony.
E. **Greig-Smith**, T.; Botany Dept., The University, Manchester 13.
E. **Gröntved**, Johannes; Botanisk Museum, Gothersgade 130, Copenhagen, K, Denmark.
E. **Grose**, J. D.; Downs Edge, Liddington, nr Swindon, Wilts.
E. **Grove**, A. T., M.A.; 2 Princess Road, Evesham, Worcs.
A. **Gudjonsson**, T. V., M.Sc.; P.O. Box 754, Reykjavik, Iceland.
E. A. **Haddow**, Dr A. J., M.B., Ch.B., B.Sc., D.P.M. & H.; Yellow Fever Research Institute, Field Box 49, Entebbe, Uganda.
A. **Hague**, Kathleen M., B.Sc.; 131 Middlewood Road, Sheffield 6.
A. **Hairston**, N. G., M.A., Ph.D.; Dept. of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. **Halket**, Miss A. C., D.Sc.; Tupra, Elstead, nr Godalming, Surrey.
E. **Hall**, R. H.; 2 Hartington Terrace, West Road, Buxton, Derbyshire.
E. **el-Halwagy**, R., B.Sc.; Dept. of Botany, University College, Gower Street, London, W.C. 1.
A. **Hamerstrom**, Dr F.; Plainfield, Wisconsin, U.S.A.
E. **Harberd**, D. J., M.Sc.; School of Agriculture, Cambridge.
A. **Hardy**, Prof. A. C., M.A., D.Sc., F.R.S.; University Dept. of Zoology, Oxford.
E. **Hare**, C. Leighton, M.Sc., Ph.D.; 21 Ashridge Avenue, North Bournemouth.

E. **Harley**, J. L., M.A., D.Phil.; University Dept. of Botany, South Parks Road, Oxford.
E. **Harper**, J. L., B.Sc.; University Dept. of Agriculture, Parks Road, Oxford.
E. **Harper**, P. C., B.Sc.; Dept. of Zoology, Bedford College, London, N.W. 1.
E. **Harris**, C. M.; Woodland Management Association Ltd., Lodge Park, Aldsworth, Glos.
A. **Harris**, L. F.; 30 Ellis Avenue, Rainham, Essex.
A. **Harris**, Prof. T. M., M.A., ScD., F.R.S.; Botany Dept., The University, Reading.
Hartland-Rowe, R. C. B.; 23 Marine Parade, Dawlish, Devon (*Associate Member*).
A. **Hartley**, P. H. T., B.Sc.; 91 Banbury Road, Oxford.
E. A. **Harvey**, Prof. L. A., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
E. **Haywood**, J., B.Sc.; 6 Pendre, Bridgend, Glamorgan.
E. **Heddle**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13 George Square, Edinburgh.
E. **Hemsley**, J. H., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Henderson**, A. G., B.Sc.; North Craigton, Culter, Aberdeenshire, Scotland.
A. **Henderson**, Miss M.; 44 Higher Bebington Road, Bebington, Cheshire.
E. A. **Hepburn**, I., M.A.; 2 Old Dryden House, Oundle, Peterborough.
E. **Hepper**, F. N., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. A. **Heslop-Harrison**, J., M.Sc., Ph.D.; Botany Dept., University College, Gower Street, London, W.C. 1.
E. A. **Heslop-Harrison**, Prof. J. W., F.R.S.; Agricultural Dept., King's College, Newcastle-upon-Tyne, 1.
A. **Hewer**, H. R., A.R.C.S., M.Sc.; Dept. of Zoology and Applied Entomology, Imperial College, London, S.W. 7.
E. **Hewetson**, C. E.; Indian Forestry Service, Jubbulpur, Central Provinces, India.
E. **Hewitt**, Miss M. S.; 92 Park Avenue, Kingston-upon-Hull, Yorks.
E. **Heywood**, V. H., B.Sc.; Botany School, Downing Street, Cambridge.
A. **Hobart**, J., B.Sc.; Dept. of Agricultural Zoology, University College, Bangor.
A. **Hobby**, B. M., M.A., D.Phil.; University Museum, Oxford.
A. **Hodgkin**, E. P.; 6 Princes Street, Mosman Park, Western Australia.
E. **Holch**, Dr A. E.; Dept. of Botany, University of Denver, Colorado, U.S.A.
E. **Hole**, Miss D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
A. **Holme**, N. A., B.A.; The Laboratory, Citadel Hill, Plymouth.
E. A. **Holmes**, P. F., M.A.; Malham Tarn Field Centre, nr Settle, Yorks.
E. **Holttum**, Prof. R. E., M.A.; University of Malaya, Cluny Road, Singapore, 10, Malaya.
E. A. **Holway**, P. H.; The Grammar School, Blackpool, Lancs.
E. **Hope-Simpson**, J. F., D.Phil.; Dept. of Botany, The University, Bristol 8.
E. **Hopkins**, B., B.Sc.; 63 Kingsway, Pendlebury, Lancs.
E. A. **Hornby**, H. E., F.R.C.V.S.; Poole Farm, Hartley, S. Rhodesia.
E. **Horne**, F. R., M.A.; Hill Farm, Lolworth, Cambs.
A. **Horridge**, G. A., B.A.; St John's College, Cambridge.
E. **Hoyle**, A. C., M.A.; 45 Green Road, Headington, Oxford.
E. **Hubbard**, C. E.; 60 Albury Avenue, Isleworth, Middlesex (*Hon. Treasurer*; receives subscriptions).
A. **Huddart**, B. J.; Shirley House, Mark Lane, Taplow, Bucks.
E. **Hughes**, F. E., B.A.; c/o Westminster Bank, High Street, Oxford.
E. **Hughes**, R. E., M.A., Ph.D.; School of Agriculture, Downing Street, Cambridge (*Hon. Secretary*).
A. **Hume**, Maj. C. W.; 284 Regent's Park Road, Finchley, London, N. 3.
A. **Humphries**, Miss D. A., B.Sc.; Butt Lane, Milton, Cambs.
E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.
A. **Hynes**, H. B., Ph.D.; Dept. of Zoology, The University, Liverpool.
E. **Irvine**, F. R., D.Sc.; 32 Tavistock Square, London, W.C. 1.
E. **Ivens**, G. W.; Mariposa, Longwell Green, nr Bristol.
E. A. **Jackson**, C. H. N., Ph.D.; Dept. of Tsetse Research, Shinyanga, Tanganyika Territory.
E. A. **Jackson**, D. S., B.A.; c/o National Bank of New Zealand, Rotorua, New Zealand.
E. **Jackson**, G., B.Sc.; 4 Rivelin Park Road, Sheffield 6.
E. **Jackson**, J. K., B.Sc.; c/o Research Division; Wad Medani, Anglo-Egyptian Sudan.
E. **Jackson**, R. M., B.Sc.; Dept. of Botany, The University, Nottingham.

A. **Jacob**, F. H.; Plant Pathology Laboratory, Milton Road, Harpenden, Herts.
A. **Jameson**, E. W., Jr., B.S., M.A.; Division of Zoology, University of California, Davis, California, U.S.A.
E. **Jameson**, J. H., M.A.; 25 Radnor Road, Handsworth, Birmingham 20.
E. **Jane**, Prof. F. W., D.Sc., F.L.S.; Highfield, Egham Hill, Englefield Green, Surrey.
E. A. **Jarrett**, T., Dept. Agric.; c/o P.O. Box 2141, Nairobi, Kenya, East Africa.
A. **Jary**, S. G.; South-Eastern Agricultural College, Wye, Ashford, Kent.
E. **Jeffares**, Miss A. A., B.A.; School of Botany, Trinity College, Dublin, Eire.
Jennings, O. E.; Carnegie Museum, Pittsburg, Pa., U.S.A. (*Hon. Life-Member*).
E. **Jensen**, H. A. P., M.A.; The Nature Conservancy, 91 Victoria Street, London, S.W. 1.
E. **Jermy**, A. C.; 'Mauveen', nr School, Strumpshaw, nr Norwich, Norfolk.
E. **Johnson**, C. S. E., B.A.; Norman Cottage, Oakham, Rutland.
A. **Johnson**, D. S., B.A.; Dept. of Zoology, Bedford College, London, N.W. 1.
E. A. **Johnson**, F. M., A.M.I.Mech.E., A.M.I.M.I.; 22 Bellevue Crescent, Duffield, nr Derby.
E. **Jones**, Dr E. W.; Imperial Institute of Forestry, Oxford.
E. **Jones**, F. R.; 19 Windermere Road, Streatham, London, S.W. 16.
E. **Jones**, Miss G. M.; The Cottage, Wraysbury, Bucks.
A. **Jones**, N. S., M.Sc.; Marine Biological Station, Port Erin, Isle of Man.
E. **Jones**, Miss V., B.Sc.; Botany Dept., University College of North Wales, Bangor.
E. **Kassas**, M. A. F. El-, M.Sc., Ph.D.; Faculty of Science, Fouad I University, Abbassieh, Cairo, Egypt.
E. **Keay**, R. W. J., M.A., F.L.S.; 40 Fairfax Road, Teddington, Middlesex.
A. **Keir**, R. S., B.Sc.; 51 Clincort Road, Glasgow, S. 2.
A. **Kellas**, Miss L. M.; 63 Carlton Place, Aberdeen.
A. **Kemp**, Miss P. B.; Clough Hall, Newnham College, Cambridge.
A. **Kendeigh**, S. C., Ph.D.; Vivarium Building, University of Illinois, Wright and Healey Streets, Champaign, Illinois, U.S.A.
A. **Kenrick**, W. E., M.A.; Metchley Abbey, Harbourne, Birmingham 17.
A. **Kettle**, D. S., M.Sc.; Dept. of Zoology, The University, Glasgow, W. 2.
E. **Kilby**, F. R., F.R.H.S.; 132 Stoke Road, Walton-on-Thames, Surrey.
E. **King**, J., B.Sc.; Sourhope, Yetholm, Kelso, Roxburghshire.
A. **King**, J. A.; Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine, U.S.A.
A. **Kitching**, J. A., M.A.; Zoology Dept., The University, Bristol 8.
E. **Klika**, Prof. Jaromír, Ph.D.; Ecole polytechnique, Praha,—Kosire 333, Czechoslovakia.
A. **Knight-Jones**, E. W., B.Sc., D.Phil.; Marine Biological Station, Bangor, N. Wales.
E. **de Kock**, Dr P. C., M.Sc.; 10 Chanonry, Old Aberdeen.
A. **Krogstad**, B. O., Asst. Prof.; Dept. of Biology, St Olaf College, Northfield, Minnesota, U.S.A.
A. **Krumholz**, L. A., Ph.D.; P.O. Box 2105, Oak Ridge, Tennessee, U.S.A.
A. **Lack**, D., Sc.D.; 91 Banbury Road, Oxford.
E. **Lambert**, Miss J. M., Ph.D.; Newnham College, Cambridge.
E. **Landon**, F. H.; c/o Dept. of Forestry, Kuala Lumpur, Malaya.
A. **Larkin**, Prof. P. A., M.A.; Dept. of Zoology, University of British Columbia, Vancouver, B.C., Canada.
A. **Laurie**, Miss E. M. O., M.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Laurie**, M. V., M.A., O.B.E.; Forest Research Station, Alice Holt, Farnham, Surrey.
E. **Lavender**, J. H., B.Sc., A.R.C.S.; 1 Manor Road, Christchurch, Hants.
E. **Lawrie**, J. J., B.Sc.; Forestry Dept., Bawku, Northern Territories, Gold Coast.
E. A. **LeCren**, E. D.; The Ferry House, Ambleside, Westmorland.
E. **Lee**, Major O. M., F.L.S.; School of Agriculture, Serdang, Selangor, Malaya.
A. **Lemare**, D. W., B.A.; Fisheries Dept., Singapore, Malaya.
E. **Leonard**, Mrs V. P.; c/o Lloyds Bank, Cambridge.
E. A. **Leston**, D., F.Z.S., F.R.E.S.; 44 Abbey Road, London, N.W. 8.
E. A. **Lewis**, C. B.; Museum of the Institute of Jamaica, Kingston, Jamaica, B.W.I.
A. **Lewis**, D. J., M.A.; Agricultural Research Service, Wad Medani, Anglo-Egyptian Sudan.
E. **Lewis**, J., B.Sc.; 52 Southfield Road, North Harrow, Middlesex.

E. A. **Lewis**, J. R., B.Sc.; Dept. of Zoology, University College of Wales, Cambrian Street, Aberystwyth.
E. A. **Lewis**, J. Spedan; Leckford Abbas, Stockbridge, Hants.
E. **Lewis**, Miss P., B.Sc., F.L.S.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Leyton**, Dr L.; Imperial Forestry Institute, South Parks Road, Oxford.
E. **Libbey**, R. P., B.Sc.; Laurel Villa, 143 Gaywood Road, King's Lynn, Norfolk.
E. **Lind**, Miss E. M., B.Sc., Ph.D.; Makerere College, P.O. Box 262, Kampala, Uganda, E. Africa.
A. **Linn**, I. J., B.Sc.; Dept. of Zoology, University College, Exeter.
E. A. **Lloyd**, L. C.; Shackerley, Wenlock Road, Shrewsbury, Shrops.
E. **Lodge**, Miss S. M., B.Sc.; Marine Biological Station, Port Erin, Isle of Man.
E. A. **London Natural History Society**; c/o C. P. Castell, 52 Graham Road, Wimbledon, London, S.W. 19.
E. **Löve**, Dr Askell, Dept. of Botany, University of Manitoba, Winnipeg, Canada.
E. **Loveless**, A. R., Ph.D.; Dept. of Botany, University College of the W. Indies, Mona, St Andrew, Jamaica, B.W.I.
E. A. **Lovett**, M., B.Sc., F.R.I.C., F.Inst.S.P.; Yorkshire Ouse River Board, 21 Park Square South, Leeds 1.
A. **Lowe**, Miss R. H., B.Sc.; Fisheries Research Laboratory, P.O. Box 343, Jinja, Uganda, E. Africa.
E. **Lüdi**, Dr W.; Gartenstrasse 12, Zollikon, Zürich, Switzerland.
A. **Lumsden**, W. H. R., B.Sc., M.B.; Virus Research Institute, P.O. Box No. 49, Entebbe, Uganda, E. Africa.
E. **Lund**, J. W. G., M.Sc., Ph.D.; Fresh Water Biological Assoc., The Ferry House, Ambleside, Westmorland.
A. **Macan**, T. T.; Stevney, Outgate, Ambleside, Westmorland.
E. A. **Macfadyen**, A.; Meopham Bank, nr Tonbridge, Kent.
A. **McHardy**, J. W., B.Sc.; Dept. of Agric. and Forest Zoology, 10 George Square, Edinburgh 8, Scotland.
A. **Mackenzie**, J. M. D., F.Z.S.; Tullach Ard, Balbeggie, Perth.
A. **MacLagan**, D. S., D.Sc., Ph.D., F.R.E.S.; West of Scotland Agricultural College, 6 Blythswood Square, Glasgow, C 2.
E. **McLean**, Prof. R. C., M.A., D.Sc.; University College, Newport Road, Cardiff, S. Wales.
E. **MacLeay**, K. N. G., B.Sc.; Gordon Memorial College, Khartoum, Anglo-Egyptian Sudan.
E. **Macleod**, Miss Anna M., B.Sc.; Heriot-Watt College, Edinburgh 1.
A. **MacLeod**, J., D.Sc.; Veterinary Laboratory, New Haw, Weybridge, Surrey.
E. **McLuckie**, J., D.Sc.; Dept. of Botany, The University, Sydney, Australia.
A. **MacLulich**, D. A., Ph.D.; 15 Bellwood Avenue, Ottawa, Ontario, Canada.
E. A. **MacNae**, W., B.Sc.; Dept. of Zoology, Rhodes University, Grahamstown, S. Africa.
E. A. **McVean**, D. N., B.Sc., B.Sc. (Agric.) N.D.A.; 27 Huntley Avenue, Giffnock, Glasgow.
A. **Madsen**, H., M.Sc.; Jagtraådets Vildtbiologiske Undersøgelser, Universitetsparken 3, Køpenhaven, Denmark.
E. **Mangham**, Prof. S., M.A.; University College, Southampton.
A. **Marples**, Prof. B. J.; The Museum, Dunedin, New Zealand.
E. **Marsden-Jones**, E. M.; Close Cottage, Littleton Panell, nr Devizes, Wilts.
E. **Mason**, E. W.; Inglenook, 63 King's Road, Richmond, Surrey.
A. **Matheson**, C.; Dept. of Zoology, National Museum of Wales, Cardiff.
E. **Matthews**, Prof. J. R., M.A.; Dept. of Botany, The University, Old Aberdeen.
E. **Meikle**, R. D., B.A., LL.B.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Mellanby**, Dr K.; The University, Ibadan, Nigeria.
E. A. **Melville**, R., Ph.D.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
Mercer, Miss H.; 21 Wheatsheaf Close, Woking, Surrey (*Associate Member*).
E. **Merton**, L. F. H., B.A.; BM/XKEG, London, W.C. 1.
E. **Messeri**, Prof. Albina; Via Bolognese 43, Firenze, Italy.
E. **Metcalfe**, Dr G., M.A.; Botany Dept., King's College, Strand, London, W.C. 2.
E. A. **Meyerriecks**, A. J.; 119–20, 146th Street, South Ozone Park 20, New York, U.S.A.
E. A. **Michelmore**, A. P. G., B.A.; Saffron Close, Chudleigh, S. Devon.
A. **Middleton**, A. D.; I.C.I. Game Services, Burgate Manor, Fordingbridge, Hants.

E. A. **Middleton**, Dr A. R.; Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
E. **Migahid**, A. M.; Botany Dept., Faculty of Science, Fouad 1 University, Abbassieh, Cairo, Egypt.
A. **Miller**, R. S., B.A.; Harvard University, Biological Labs., 16 Divinity Avenue, Cambridge 38, Mass., U.S.A.
A. **Milne**, Dr A., M.A.; Dept. of Agriculture, King's College, Newcastle-upon-Tyne 2.
E. A. **Milne-Redhead**, E. W. B. H., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Mirams**, R. V., M.Sc.; 555 Manukau Road, Epsom, Auckland, New Zealand.
E. **Misra**, Dr R.; Dept. of Botany, University of Saugor, Saugor, Central Provinces, India.
E. **Mitchell**, G. F., M.A.; Dept. of Irish Archaeology, Trinity College, Dublin, Eire.
E. **Mohan**, N. P., M.A., B.Sc.; c/o Imperial Bank of India, Simla, India.
E. **Montasir**, Professor Abd El-Halim, Ph.D., M.S.; Faculty of Science, Ibrahim University, Orman, Giza, Egypt.
A. **Montford**, H. M., B.Sc.; 23 Mount Side, Guildford, Surrey.
A. **Moon**, Prof. H. P., M.A.; Dept. of Zoology, University College, Leicester.
E. **Mooney**, H. F., C.I.E., O.B.E., Sc.D., F.L.S.; British Middle East Office, British Legation, Beirut, Lebanon.
E. A. **Moore**, Barrington; Stone Acre, Corfe, Taunton.
E. **Moore**, Mrs M., B.Sc.; 17 Staplehurst Road, Hall Green, Birmingham 28.
A. **Moore**, N. W., B.A.; Dept. of Zoology, University of Bristol, Bristol 8.
E. **Moore**, R. M., M.Sc.; Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T., Australia.
A. **Morley**, B. D. W., B.A., F.L.S.; Institute of Animal Genetics, West Mains Road, Edinburgh 9.
E. A. **Moynahan**, E. J., M.R.C.S.; Wayside, Jordans, Beaconsfield, Bucks.
A. **Muir**, R. C.; Zoology Dept., Downing Street, Cambridge.
A. **Murphy**, D. H.; Zoology Dept., South Road, Durham.
A. **Neal**, E. G., B.Sc.; 2 Bishop's Mead, Kingston Road, Taunton.
E. **Neales**, T. F.; Worcester College, Oxford.
A. **Nelmes**, E. M., B.A.; 27 Westbourne Avenue, Acton, London, W. 3.
E. **Nelmes**, Miss S.; 48 Defoe Avenue, Kew, Surrey.
E. **Newbould**, P. J.; Leagues Crowborough, Sussex.
E. A. **Newman**, Leslie F., M.A.; 45 London Road, Bishop's Stortford, Herts.
E. **Newton**, Miss L. M., B.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. A. **Newton**, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, University College of Wales, Aberystwyth, Wales.
A. **Newton**, Dr R. G.; 102 New Church Road, Hove 3, Sussex.
A. **Nichols**, J. E., Ph.D.; Dept. of Agriculture, University College of Wales, Aberystwyth.
A. **Nicholson**, E. M.; 13 Upper Cheyne Row, London, S.W. 3.
E. **Nicholson**, I. A., B.Sc.; Grassland Dept., N. Scotland College of Agriculture, 41½ Union Street, Aberdeen.
E. A. **Nielsen**, C. O., D.Phil.; Naturhistorisk Museum, Aarhus, Denmark.
E. **Norman**, M. J. T., B.Sc.; Grassland Research Station, Hurley, nr. Maidenhead, Berks.
A. **Norris**, K. R., M.Sc.; C.S.I.R.O. Entomology Division, P.O. Box 109 City, Canberra, A.C.T., Australia.
A. **North**, Major M. E. W., B.A.; c/o Secretariat, Nairobi, Kenya, E. Africa.
E. **Northumberland, Durham & Newcastle-on-Tyne Nat. Hist. Soc.**; Hancock Museum, Barras Bridge, Newcastle-on-Tyne 2.
E. **Oliver**, W. R. B., D.Sc.; 26 Ventnor Street, Seatown, Wellington, E. 5, New Zealand.
A. **Omer-Cooper**, Prof. J., M.A., M.Sc.; Rhodes University College, Grahamstown, S. Africa.
E. A. **Orr**, H. R.; Technical College, Longport Street, Canterbury.
E. **Orr**, M. Y.; Royal Botanic Gardens, Edinburgh 4.
E. **Osborn**, Prof. T. G. B.; University Dept. of Botany, South Parks Road, Oxford.
E. **Osmaston**, H., M.A.; Forest Office, Fort Portal, Uganda, E. Africa.
E. **Osvald**, Prof. K. Hugo; Royal Agricultural College, Uppsala 7, Sweden.
E. **Ovington**, J. D., Ph.D.; Nature Conservancy, 83–91 Victoria Street, London. S.W. 1.
A. **Pallant**, D., B.Sc.; 8 Andover Road, Southsea, Hants.

E. A. **Park**, Dr O.; Zoological Dept., Northwestern University College of Liberal Arts, Evanston, Ill., U.S.A.
E. **Parke**, Dr Mary; The Laboratory, Citadel Hill, Plymouth.
E. **Parker**, R. E., B.Sc.; Dept. of Botany, University College of North Wales, Bangor.
A. **Parry**, D. A., Ph.D.; King's College, Cambridge.
A. **Paulson**, C. W. G.; c/o Monotype Corporation, Ltd., Salfords, Redhill, Surrey.
A. **Peacock**, Prof. A. D., D.Sc., F.R.S.E.; University College, Dundee.
A. **Peake**, J. F.; 17 Tillet Road, Norwich.
E. **Pearsall**, Prof. W. H., F.R.S.; Botany Dept., University College, Gower Street, London, W.C. 1.
E. A. **Pearson**, J., D.Sc.; Tasmanian Museum and Art Gallery, Hobart, Tasmania.
E. **Pearson**, M. C., B.Sc.; 17 Norman Road, Sale, Manchester.
E. **Penston**, Dr Norah L., F.L.S.; Bedford College, Regent's Park, London, N.W. 1.
A. **Pentelow**, F. T. K.; Old Slade Lane, Iver, Bucks.
A. **Percival**, Prof. E.; Canterbury University College, Christchurch, New Zealand.
A. **Perkins**, E. J.; 122 Hainault Road, Leytonstone, London, E. 11.
E. **Perraton**, C. J., B.A.; Munro College, Jamaica, B.W.I.
E. **Perrin**, R. M., B.A.; School of Agriculture, Cambridge.
E. **Perring**, F. H., B.A.; 58 Warkworth Terrace, Cambridge.
E. **Petch**, C. P., M.A., M.B.; Sundial House, North Wootton, King's Lynn, Norfolk.
E. **Peterken**, J. H. G., F.L.S.; 73 Forest Drive East, Leytonstone, London, E. 11.
E. **Phillips**, Miss M. E., M.Sc.; Dept. of Botany, The University, Manchester 13.
E. **Pichi-Sermolli**, Prof. R.; Istituto Botanico dell' Universita, Via Lamarmora 4, Firenze, Italy.
E. **Pielou**, E. C. (Mrs), B.Sc.; c/o Dominion Entom. Lab. Summerland, British Columbia.
A. **Pielou**, Dr D. P.; Entomological Laboratory, Summerland, British Columbia.
E. **Piemeisel**, R. L.; P.O. Box 826, Twin Falls, Idaho, U.S.A.
E. **Pigott**, C. D., B.A.; Clevedon, Harestone Hill, Caterham, Surrey.
A. **Pitelka**, F. A., Ph.D.; Museum of Vertebrate Zoology, University of California, Berkeley 4, California, U.S.A.
E. **Pitman**, P. B., B.Sc.; 98 Queen's Road, Richmond, Surrey.
E. **Poel**, Dr L. W.; Dept. of Botany, The University, St Andrews.
E. **Polunin**, Prof. N., D.Phil., D.Sc.; Dept. of Botany, McGill University, Montreal, Canada.
E. A. **Poore**, M. E. D.; The Rectory, Landbeach, Cambs.
E. A. **Potts**, W. H., M.A.; Dept. of Tsetse Research, Shinyanga, Tanganyika Territory.
E. A. **Pough**, R. H.; American Museum of Natural History, Central Park West at 79th Street, New York 24, N.Y., U.S.A.
E. **Powell**, Miss Doris, M.Sc.; Aldersyde, Reigate, Surrey.
E. A. **Powell**, H. T., B.Sc.; Marine Station, Millport, Isle of Cumbrae, Scotland.
A. **Pradhan**, Dr S.; Entomology Division, Indian Agricultural Research Institute, New Delhi, India.
E. A. **Praeger**, Dr R. Lloyd; Royal Irish Academy, 19 Dawson Street, Dublin.
E. **Pratt**, Dr C. A.; Botany Dept., Imperial College of Science and Technology, London, S.W. 7.
A. **Preston**, F. W., Preston Laboratories, Box 847, Butler, Pennsylvania, U.S.A.
A. **Price**, Miss K. L. H.; Hillside, Headington Hill, Oxford.
A. **Price Jones**, Dr D.; Fernhurst, nr Haslemere, Surrey.
A. **Prideaux**, R. C.; Claigan, Dunvegan, Isle of Skye.
E. **Prime**, C. T., M.A., F.L.S.; 147 Upper Selsdon Road, Sanderstead, S. Croydon, Surrey.
E. **Proctor**, M. C. F., B.A.; Botany School, Downing Street, Cambridge.
E. **Puri**, Dr G. S.; Forest Research Institute, P.O. New Forest, Dehra Dun (U.P.), India.
E. **Quist-Arcton**, E. A.; Brasenose College, Oxford.
A. **Radway Allen**, K.; P.O. Box 202, Fisheries Laboratory, Marine Dept., Wellington, New Zealand.
E. **Raggio**, M.; 25 de Mayo 316, Esc. 2, Piso 1, Buenos Aires, Argentina.
E. **Rains**, A. B., B.Sc.; 28 Vicarage Lane, Humberstone, Leicester.
E. **Ramsbottom**, J., M.A., O.B.E.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
A. **Rand**, R. W., B.Sc.; c/o Union Govt., Guano Is., 32 Riebeck Street, Cape Town, S. Africa.
E. **Ranwell**, D. S., B.Sc.; Dept. of Botany, University College of North Wales, Memorial Buildings, Bangor, Caern.

E. **Rao**, Prof. L. N., Ph.D., F.R.M.S., F.A.Sc.; Dept. of Botany, Mysore University, Central College, Bangalore, India.
E. **Ratcliffe**, D. A., B.Sc.; 73 Newton Road, Carlisle.
A. **Ratcliffe**, F. N., B.A.; Council for Scientific and Industrial Research, P.O. Box 109, Canberra, A.C.T., Australia.
A. **Raw**, Frank, B.Sc.; Rothamsted Experimental Station, Harpenden, Herts.
A. **Raymont**, Prof. J. E. G., B.Sc., A.M.; Dept. of Zoology, University College, Southampton.
E. **Rees**, J., B.A., M.Sc.; N.A.A.S., Min. of Agriculture and Fisheries, University College, Cardiff.
E. **Rees**, T. Kenneth; Board of Trade, Neville House, Page Street, London, S.W. 1.
E. **Rees**, W. J., Ph.D.; Botany Dept. The University, Edgbaston, Birmingham 15.
E. A. **Rees-Wright**, Rev. Prof. W., Ph.D.; Dept of Biology, Memorial University College, St John's, Newfoundland.
E. **Regel**, Dr C.; University College of Arts and Sciences, Baghdad, Iraq.
E. A. **Reid**, D. A., B.Sc.; 19 High Street, Leighton Buzzard, Beds.
A. **Reid**, D. M.; Science Schools, Harrow-on-the-Hill, Middlesex.
E. A. **Reid**, R. E. H., B.Sc.; Pentryn, Bois Lane, Chesham Bois, Bucks.
E. A. **Renouf**, Prof. L. P. W.; University College, Cork, Eire.
A. **Reynoldson**, T. B., Ph.D.; Dept. of Zoology, University College of North Wales, Bangor, N. Wales.
E. **Rhodes**, Prof. A. D.; Forestry Dept., Massachusetts State College, Amherst, Mass., U.S.A.
A. **Ribbands**, C. R., M.A.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Ribbons**, B. W.; 28 Boundary Road, Norwich, Norfolk.
E. A. **Richards**, O. W., M.A., D.Sc.; Zoology Dept., Imperial College of Science, S. Kensington, London, S.W. 7.
E. **Richards**, P. T.; New College, Oxford.
E. **Richards**, Prof. P. W., M.A., Ph.D.; Dept. of Botany, University College, Bangor.
E. **Richards**, Mrs S. A., M.A.; Coed Menai, Upper Bangor, Caern.
A. **Richards**, Dr W. S.; c/o M.C.P.S., Wad El Hur, Anglo-Egyptian Sudan.
A. **Richdale**, L. E.; 23 Skibo Street, Kew, Dunedin, New Zealand.
A. **Rintoul**, Miss L. J.; Balsusney, Upper Largo, Fife.
E. **Ritchie**, J. C., B.Sc.; 165 Broomhill Road, Aberdeen, Scotland.
A. **Roberts**, B. B.; Scott Polar Research Institute, Lensfield Road, Cambridge.
A. **Roberts**, H., B.Sc.; Soth Stoneham House, Swaythling, Southampton.
E. **Roberts**, H. A., B.Sc.; Strebor, Springfield Road, Ulverston, Lancs.
E. **Roberts**, Prof. R. Alun; Agricultural Dept., University College, Bangor, N. Wales.
E. **Robertson**, A. G., B.Sc.; Botany Dept.. The University, Old Aberdeen.
E. **Robertson**, Miss E. T., B.Sc., F.G.S.; Dept. of Botany, The University, Old Aberdeen.
E. **Robertson**, R. N.; The Botany Dept., The University, Sydney, Australia.
E. **Rorison**, I. H.; 32 Wansunt Road, Bexley, Kent.
E. **Rosayro**, R. A. de, B.A., B.Sc.; Forest Dept., P.O. Box 500, Colombo, Ceylon.
E. **Rose**, F.; The Forge House, East Malling, Maidstone, Kent.
E. **Rosenberg**, Dr Marie (Mrs Burton); *see under* Dr M. B. Burton.
E. **Ross**, R., B.A.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
A. **Rothschild**, The Hon. Miriam; Ashton Wold, Peterborough.
E. **Round**, F. E., B.Sc.; Botany Dept., The University, Liverpool 3.
E. A. **Rowntree**, J. R. B., M.A.; Hilla Green Farm, Hackness, Scarborough, Yorks.
E. **Rübel**, Dr E.; Zürichbergstrasse 38, Zürich 44, Switzerland.
E. **Russell**, Dr E. W.; Dept. of Agriculture, Parks Road, Oxford.
E. **Russell**, Dr R. S.; Dept. of Agriculture, Parks Road, Oxford.
E. **Russell-Wells**, Miss B., Ph.D.; Biology Dept., Lancing College, Shoreham, Sussex.
E. **Rutter**, Dr A. J.; Botany Dept., Imperial College of Science, S. Kensington, London, S.W. 7.
A. **Rzóska**, Julian R. D.; Gordon Memorial College, Khartoum, A.-E. Sudan.
E. A. **Sale**, G. N., B.Sc.; The Nature Conservancy, 83–91 Victoria Street, London, S.W. 1.
E. **Salisbury**, Sir Edward J., C.B.E., D.Sc., F.R.S.; Royal Botanic Gardens, Kew, Surrey.
A. **Salt**, G., D.Sc., Sc.D.; King's College, Cambridge.
A. **Sandison**, Miss E. E., B.Sc.; Dept. of Zoology, West Mains Road, Edinburgh 9.

E. **Sangster**, R. G.; Assistant Conservator of Forests, P.O. Box 31, Entebbe, Uganda.
A. **Sankey**, J. H. P., B.Sc.; Juniper Hall Field Centre, Dorking, Surrey.
E. **Sansom**, Miss J. M., B.Sc.; 149 Sandbanks Road, Parkstone, Dorset.
E. **Santapau**, Rev. H., Ph.D.; St Xavier's College, Cruikshank Road, Bombay 1, India.
E. **Sappa**, Dr Francesco; Istituto Botanico, Viale Mattioli 31, Turin, Italy.
E. A. **Saunders**, J. T., M.A.; Christ's College, Cambridge.
A. **Savage**, R. M.; Rosendaui, Parkgate Crescent, Hadley Wood, Barnet, Herts.
E. **Schelpe**, E. A. C. L. E., M.Sc.; Wadham College, Oxford.
E. **Scurfield**, G., Ph.D.; Botany Dept., Manchester University.
E. A. **Segadas-Vianna**, F., B.Sc.; Rua Rainha Guilhermina, 83 Leblon, Rio de Janeiro, Brazil.
E. **Shaw**, Miss M. S., B.Sc.; Woodlea, Honley, nr Huddersfield.
E. **Sheldon**, J., B.Sc.; 'Hazeldene', 45 Victoria Road, Gorleston-on-Sea, Norfolk.
A. **Shelford**, Prof. Victor E.; Vivarium Building, Wright and Healey Streets, Champaign, Ill., U.S.A.
E. **Sherrin**, W. R.; South London Bot. Inst., 323 Norwood Road, Herne Hill, London, S.E. 24.
E. **Sherwood**, E. G. P., M.A.; c/o I.C.I. Ltd., 12 Upper Belgrave Street, London, S.W. 1.
E. **Simmonds**, N. W., M.A.; Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I.
E. **Simpson**, N. Douglas, M.A., F.L.S.; 3 Cavendish Road, Bournemouth, Hants.
E. **Singh**, B. N., D.Sc.; Institute of Crop Physiology, 1 A Sultanpur Road, Lucknow, India.
A. **Singh**, C. P., B.Sc., M.Sc.; Zoology Dept. University College, Southampton.
E. A. **Skellam**, J. G., M.A.; 30 The Little Boltons, S. Kensington, London, S.W. 10.
E. **Skene**, Prof. Macgregor, D.Sc.; The University, Bristol 8.
E. **Small**, Prof. J., D.Sc.; Queen's University, Belfast, N. Ireland.
E. **Smith**, P. M. (Miss), B.Sc.; Osmotherley, Bromsgrove, Worcs.
A. **Smith**, Dr R. F., M.S., Ph.D.; 112 Agriculture Hall, University of California, Berkeley 4, California, U.S.A.
A. **Smyly**, W. J. P., B.Sc.; Ferry House, Far Sawrey, Ambleside, Westmorland.
A. **Solomon**, M. E., M.Sc.; 50 Dolphin Road, Slough, Bucks.
A. **Southern**, H. N., B.A.; Bureau of Animal Population, Botanic Gardens, High Street, Oxford.
E. **Sowter**, F. A.; 9 North Avenue, Leicester.
E. A. **Spater**, E. G., F.C.I.I.; 1 Threadneedle Street, London, E.C. 2.
E. A. **Spence**, A. C., M.R.C.S., L.R.C.P.; 7 Selwood Terrace, Onslow Gardens, London, S.W. 7.
E. **Spooner**, G. M., M.A., M.B.E.; Marine Biological Laboratory, Citadel Hill, Plymouth.
A. **Spooner**, Mrs G. M.; Fiveoaks, Crapstone, Yelverton.
E. **Sporne**, K. R., M.A., Ph.D.; The Botany School, Cambridge.
E. A. **Stamp**, Prof. L. Dudley; 93 Sloane Street, London, S.W. 1.
E. **Stanbury**, Miss F. A.; Plymouth and Devonport Technical College, Tavistock Road, Plymouth.
A. **Stephen**, Dr A. C.; Royal Scottish Museum, Edinburgh.
A. **Stephenson**, J. W., B.Sc.; Entomology Dept., Rothamsted Experimental Station, Harpenden, Herts.
A. **Stephenson**, Prof. T. A., D.Sc.; Dept. of Zoology, University College of Wales, Aberystwyth.
A. **Stephenson**, Prof. W.; Dept. of Zoology, University of Queensland, Brisbane, Australia.
E. **Stevens**, A. J., B.A.; 25 Wings Road, Upper Hale, Farnham, Surrey.
A. **Stevens**, D. M.; Dept. of Zoology, West Mains Road, Edinburgh 9.
E. **Stevenson**, Miss E. H.; 28 Foxcombe Road, Weston, Bath, Somerset.
E. **Stewart**, Dr R. R., M.A.; Gordon College, Rawalpindi, Pakistan.
E. **Stiles**, Prof. W., M.A., Sc.D., F.R.S.; 'Elsley Lodge', Tilehurst on Thames, Reading.
A. **Stower**, W. J., B.Sc.; 53 Polsloe Road, Heavitree, Exeter.
E. A. **Streets**, R. J., M.A.; c/o Forestry Dept., Nicosia, Cyprus.
A. **Strickland**, A. H., M.A.; Plant Path. Lab., Ministry of Agriculture, Milton Road, Harpenden, Herts.
E. **Subrahmanyan**, R., B.Sc., M.Sc., Ph.D.; 52 Choolai High Road, Madras 7, India.
E. A. **Summerhayes**, V. S., B.Sc.; 22 West Park Avenue, Kew Gardens, Richmond, Surrey (*Hon. Treasurer*).
E. **Suvatabandhu**, Kasin, B.Sc.; Botanical Section, Dept. of Agriculture, Bangkok, Thailand (Siam).

E. **Suxena**, M. R., M.Sc.; Botany Dept., Osmania University, Hyderabad, Deccan, India.
E. **Swabey**, C.; Forest Department, Entebbe, Uganda, E. Africa.
E. **Swann**, E. L.; 282 Wootton Road, King's Lynn, Norfolk.
A. **Swynnerton**, G. H.; Game Preservation Dept., Nyamungu, Moshi, Tanganyika Territory.
E. **Tansley**, Prof. Sir Arthur G., F.R.S.; Grantchester, Cambridge (*Hon. Life-Member*).
A. **el Tayeb Abdel Maksoud**, A., B.Sc.; c/o Khartoum University College, Khartoum, Sudan.
A. **Taylor**, D. J., B.Sc.; Woodside, Usk, Monmouthshire.
E. **Taylor**, F. J., M.Sc.; Dept. of Botany, Queen Mary College, Mile End Road, London, E. 1.
E. **Taylor**, Miss M. H., B.Sc.; Belmont Farm, Clarendon, nr Salisbury, Wilts.
E. **Taylor**, G., D.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Taylor**, Miss J., M.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Tedd**, H. Griffith; Bottor Cottage, Hennock, Bovey Tracey, Devon.
A. **Tevis**, Lloyd P.; Box 1416, Carmel, California, U.S.A.
E. **Thoday**, Prof. D., M.A., Sc.D., F.R.S.; Botany Department, The University, Leeds, 2.
E. A. **Thomas**, A. K., B.Sc.; 2 Norwood Road, Shipley, Yorks.
E. **Thomas**, A. S., D.Sc.; Goodings Cottage, Woodland St Mary, Newbury.
A. **Thomas**, J. F., B.A.; 17 Belle Grove Terrace, Spital Tongues, Newcastle-on-Tyne 2.
E. **Thomas**, H. Hamshaw, M.B.E., Sc.D., F.R.S.; Botany School, Cambridge.
E. **Thomas**, Miss M. K., B.Sc.; 33 Centurion Drive, Meols, Cheshire.
A. **Thompson**, H. V., B.Sc.; Bureau of Animal Population, Botanic Gardens, High Street, Oxford.
A. **Thompson**, Mrs Una, B.Sc.; 21 Ivanhoe, Monkseaton, Northumberland.
A. **Thomsen**, H. P., Ph.D., M.S.; Dept. of Zoology, University of Wisconsin, Madison, Wis., U.S.A.
Thornton, I. W. B., B.Sc.; 13 Lane Ends Terrace, Hipperholme, Halifax (*Associate Member*).
E. **Thorp**, Mrs D. A.; c/o Prof. Thorp, Sydney University, N.S.W., Australia.
Thorpe, W. H., Sc.D.; Jesus College, Cambridge (*Associate Member*).
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A. **Tinbergen**, Dr L.; Zoologisch Laboratorium, Groningen, Holland.
E. **Tincker**, M. A. H., M.A., D.Sc.; Hort. Dept., North of Scotland College of Agric., 41½ Union Street, Aberdeen.
A. **Tjønneland**, A.; Zoologisk Laboratorium, The University, Bergen, Norway.
E. **Todd**, Miss M. A., M.Sc.; c/o Agent General for Victoria, Victoria House, Strand, London, W.C. 2.
E. A. **Tonolli**, Dr V.; Istituto Italiano di Idrobiologia, Pallanza (Novara), Italy.
A. **Toschi**, Prof. A.; Laboratorio di Zoologia, Via S. Giacomo 9, Bologna, Italy.
E. A. **Trapnell**, C. G., B.A.; E. African Agric. & Forestry Res. Organ., P.O. Box 21, Kikuyu, Kenya.
E. **Troll**, Prof. C.; Geographical Dept., University of Bonn, Bonn, Germany.
E. A. **Tucker**, D. G., Ph.D.; 'Three Ways', 115 Clearmount Road, Rodwell, Weymouth, Dorset.
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A. **Turner**, Miss M. A.; 4 Orchard Gardens, Dunsford Road, Exeter.
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A. **Tutin**, Mrs T. G., Ph.D.; University College, Leicester.
E. **Tüxen**, Prof. Reinhold; Schinnaerlandsstr. 6, Stolzenau/W., Germany.
E. **Tyler-Smith**, M. A.; Strathallan, Broadway, Southbourne, Bournemouth.
A. **Uvarov**, B. P., C.M.G., D.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Valentine**, Prof. D. H., Ph.D.; University Dept. of Botany, Science Laboratories, South Road, Durham.
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A. **Vincent**, Miss M. H., B.Sc.; 17 Saddler Street, Durham.
A. **Vizoso**, Mrs M. R., B.A.; 11 Churchdale Court, Harvard Road, Chiswick, London, W. 4.
A. **Vogt**, W.; 501 Madison Avenue, New York 22, N.Y., U.S.A.
A. **Voûte**, Dr Alexander D.; 'Mariendaal', Oosterbeek, Holland.
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E. **Wadham**, Prof. S. M.; School of Agriculture, Melbourne University, Australia.
A. **Wagge**, Miss L. E., B.Sc., Ph.D.; 192 Lichfield Court, Richmond.
E. **Walker**, D., B.Sc.; 21 Panton Street, Cambridge.
E. **Walker**, F. T., B.Sc.; Institute of Seaweed Research, Inveresk Gate, Musselburgh, Midlothian.
E. A. **Wallace**, T. J.; Goodmans, Furley, Membury, nr Axminster, Devon.
A. **Waloff**, Miss Nadejda, Ph.D.; Dept. of Zoology, Imperial College of Science, Prince Consort Road, London, S.W. 7.
E. **Walters**, S. M., B.A.; Botany School, Downing Street, Cambridge.
E. **Walton**, Prof. J.; Dept. of Botany, The University, Glasgow.
E. **Wanstall**, P. J.; 54 Matlock Road, Brighton 5, Sussex.
E. **Warburg**, E. F., M.A., Ph.D.; University Dept. of Botany, South Parks Road, Oxford.
A. **Ward**, J. D. U.; Rodhuish, Watchet, Somerset.
E. **Watkins**, G., B.Sc.; Dyffryn, 13 Glanyrafon Road, Sketty, Swansea.
A. **Watson**, J. S., B.A., D.S.I.R. Animal Ecology Section, Wellington, New Zealand.
E. **Watson**, W., D.Sc.; Cedene, Cheddon Road, Taunton, Somerset.
E. A. **Watson-Walker**, J., B.Sc.; 12 The Bowley, Diseworth, Derby.
E. A. **Watt**, A. S., Ph.D.; The Botany School, Cambridge.
E. A. **Watt**, Mrs W. Boyd; 39 Christchurch Road, Bournemouth, Hants.
E. A. **Watterson**, J. G., B.Sc.; Tsetse Survey and Reclamation Dept., Box 396, Arusha, Tanganyika Territory.
E. **Webb**, Prof. D. A., Ph.D.; School of Botany, Trinity College, Dublin, Eire.
E. A. **Weese**, Prof. A. O.; Dept. of Zoological Sciences, University of Oklahoma, Norman, Oklahoma, U.S.A.
A. **Weiss**, Prof. F. E., D.Sc., F.R.S.; 73 Longton Avenue, Sydenham, London, S.E. 26.
A. **Werth**, Miss I.; Dept. of Zoology, The University, Leeds 2.
E. **West**, Dr Cyril; The Cowl House, Holt Wood, Aylesford, Kent.
E. **West**, R. G.; 34 Elwill Way, Beckenham, Kent.
E. A. **Wheatley**, A. R., B.Sc.; Greenacre, Orchard Way, Esher, Surrey.
E. **White**, D. S., B.Sc.; 3 Snowdon Villas, The Crescent, Bangor, N. Wales.
E. **White**, F., B.A.; Imperial Forestry Institute, South Parks Road, Oxford.
A. **White**, Miss K. M., B.Sc., Ph.D.; Glastonbury, Boyn Hill Avenue, Maidenhead, Berks.
E. A. **White**, O. M.; 78 Eastdale Road, Nottingham.
A. **White**, P. H. F., M.A.; Science Schools, Harrow School, Harrow, Middlesex.
E. **Whitehead**, F. H., B.A.; University Dept. of Botany, South Parks Road, Oxford.
E. **Whitehouse**, H. L. K., M.A., Ph.D.; Botany School, Cambridge.
E. **Whyte**, Dr R. O.; c/o Plant Prod. Branch, F.A.O. Viale delle Terme di Caracalla, Rome, Italy.
E. **Wiehe**, P. O.; Dept. of Agriculture, Zomba, Nyasaland.
E. **Wilkins**, D. A., B.Sc.; 'Sherwood'. 22 Courtenay Park, Newton Abbot.
E. **Wilkins**, W. C., B.Sc.; 17 East Avenue, Kenfig Hill, Bridgend, Glamorgan.
A. **Williams**, C. B., Sc.D.; Rothamsted Experimental Station, Harpenden, Herts. (*President*).
E. **Williams**, O. G., B.Sc.; Ministry of Agriculture and Fisheries, Shardlow Hall, Shardlow, nr Derby.
Williams, R. D., B.Sc., Ph.D.; 92 Loxley Road, Stratford-upon-Avon, Warwicks. (*Associate Member*).
E. **Williams**, Mrs S. S., B.Sc.; Grassland Research Station, Drayton, Stratford-on-Avon, Warwicks.
E. A. **Williamson**, M. H.; Fairfield, Pullen's Lane, Oxford.

E. **Wilson**, I. E., B.Sc.; 73 Greenburn Drive, Bucksburn, Aberdeenshire.
E. **Wilson**, J. M., M.A.; St John's College, Oxford.
E. **Wilson**, J. W.; Magdalen College, Oxford.
A. **Wilson**, Mrs P. M. W., M.A.; 7 Denmark Road, Reading.
E. **Wilson Mayne**, W., B.Sc.; Scientific Officer, Messrs Kanan Devans Hills Produce Co. Ltd., Munnar P.O., Travancore, India.
A. **Winterbottom**, J. M., Ph.D.; Box 150, Livingstone, N. Rhodesia.
E. **Wood**, G. H. S., M.A.; c/o Imperial Forestry Institute, South Parks Road, Oxford.
E. A. **Woodcock**, G. S., F.R.E.S.; Ivy House, Bishop's Hall, Brentwood, Essex.
E. **Woodhead**, Norman, M.Sc.; Dept. of Botany, University College, Bangor, N. Wales.
E. A. **Worden**, Prof. A. N., M.A., B.Sc.; Cromwell House, Huntingdon.
E. **Wright**, A. C. S.; D.S.I.R. Soil Bureau, Aotea Quay, Wellington, New Zealand.
E. **Wright**, Mrs B. I., B.Sc.; 'Ecclesfield', 176 Stockbridge Road, Winchester.
E. **Wright**, Dr F. R. Elliston; Braunton, N. Devon.
A. **Yapp**, W. B., M.A.; Dept. of Zoology, The University, Edgbaston, Birmingham 15.
E. **Young**, B. S.; 29 Montana Road, Tooting Bec, London, S.W. 17.
E. **Zehetmayr**, J. W. L.; 28 Groathill Avenue, Edinburgh 4.
E. **Zinderen Bakker**, Dr E. M. van; University of the Orange Free State, Bloemfontein, S. Africa.
E. **Zohary**, Dr M.; Dept. of Botany, Hebrew University, Jerusalem.

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